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DENSITY-DEPENDENT SEARCHING TIME: IMPLICATIONS IN SURPLUS-PRODUCTION MODELS[1]

RICHARD E. CONDREY[2]

ABSTRACT

An initial theoretical consideration is presented to show how density-dependent searching time can be incorporated into surplus-production models of fisheries. A simple simulation is used to demonstrate the management implications associated with failure to account for this parameter in fisheries where handling time reduces the total time initially available for searching.

The failure to measure density-dependent searching time in assessing fishing effort can lead to erroneous conclusions concerning the collapse of a fishery. In this paper, I will develop my argument using two simple models: Graham's equilibrium yield model (Graham 1935; Ricker 1975) and Holling's (1959b) "disk" equation. I will conclude by drawing parallels between this simple theoretical treatment and patterns that have been observed in searching fisheries.

DEVELOPMENT OF THE MODEL

I begin with the normal definition of the instantaneous rate of fishing mortality, F, as

$$F = q \cdot f = C/N \qquad (1)$$

where q is the instantaneous catchability coefficient and is the proportion of the stock (N) that is caught (C) by one unit of fishing effort (f); this fishing effort (f) is the total gear in use for a specific time (Ricker 1975). Following the example of Beddington (1979) and Fowler (1980), I depart from the normal treatment of f, by considering

$$f = f' \cdot t'_s \qquad (2)$$

where f' is a physical measure of the total fishing gear in use and t'_s is the proportion of the total fishing time (t') which is available for and used in searching.

If searching time is a constant, independent of stock abundance N, then a linear relationship is normally expected between C/f' (or C/f) and N up to some theoretical limit, as in a Holling (1959a) Type I curve (Fig. 1A) or in the Palohemio and Dickie (1964) model.

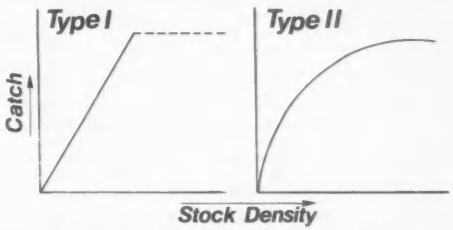

FIGURE 1.—Two types of functional responses of catch to stock density, after Holling (1959a).

If, however, fishermen must expend a substantial amount of time in harvesting the catch once it is sighted, this handling time (t'_h) will reduce the time initially available for searching (e.g., Gulland 1956, 1964; Rothschild and Suda 1977). Holling (1959b) describes one such dependence of t'_s on N as

$$t'_s = t' - t'_h\,(C/f'). \qquad (3)$$

Equation (3) describes a curvilinear decline in C/f' with increasing stock abundance (Fig. 1B). Substituting Equation (3) into Equation (2) into Equation (1), we obtain

$$F = q \cdot f' \cdot (t' - t'_h \cdot C/f'), \qquad (4)$$

which can be arranged to

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$$1 = \frac{q \cdot f' \cdot t'}{F} - \frac{q \cdot f' \cdot t'_h \, (C/f')}{C/N}$$

$$F = \frac{q \cdot f' \cdot t'}{1 + q \cdot t'_h \cdot N}.$$

Inserting this definition of F as a substitute in Graham's equilibrium yield model, then

$$Y_e = B_e \cdot F_e = k \cdot B_e \cdot (B_\infty - B_e)/B_\infty$$

$$= B_e \cdot q \cdot t' \cdot f'/(1 + q \cdot t'_h \cdot B_e) \quad (5)$$

where B_∞ is the maximum stock biomass, k is the instantaneous rate of increase of the stock as density approaches zero, B_e is the stock mass at an equilibrium position, Y_e is the equilibrium yield, and F_e is the fishing mortality rate which maintains the stock at B_e (Ricker 1975).

As expected a plot of Y_e against B_e or F_e will yield a symmetrical hyperbola, Figure 2A; a plot of q against B_e will denote that q is a constant regardless of the relative magnitude of t'_h to t'. This is not the case, however, if we ignore the effect that stock density has on searching time. For example, a plot of Y_e against $f' \cdot t'$ results in an asymmetrical hyperbola skewed to the right, Figure 2B. The distortion increases as the ratio t'_h/t' approaches 1 and is a result of the increased time the fleet must spend searching for fish as population biomass approaches zero, Figure 2C. Additionally, if searching time is assumed to be independent of stock abundance, q will be incorrectly measured as $q/(1 + q \cdot t'_h \cdot B_e)$ and will appear to be inversely related to population density, Figure 2D.

Note that when $t'_h > 0$, $f' \cdot t'$ will not peak at $B_e = 0$ (for the situation described in Equation (5)). Instead, it will peak at some intermediate level of B_e and will then decline, Figure 2E. Thus, even for the hypothetical equilibrium fishery, $f' \cdot t'$ would have to "voluntarily" decline from a maximum level as B_e approaches zero.

DISCUSSION

The assumptions inherent in Equation (5) limit its direct application as a qualitative model of existing fisheries. However, the general behavior described in Figure 2B, D has been noted in several recent papers (Fox 1974; Pope and Garrod 1975; Schaaf 1975b; MacCall 1976; Ultang 1976; Garrod 1977; Peterman 1980; Peterman and Steer 1981; Bannerot and Austin 1983). Two important examples occur with the Pacific sardine and Atlantic menhaden fisheries.

In their analysis of the available catch and effort data on the California based fishery on Pacific sardine, Fox (1974) and MacCall (1976) were forced to relax the usual restriction of a constant catchability coefficient which is independent of population size. Rather, they applied a density-dependent catchability coefficient of the form

$$q = \alpha N^{\beta} \quad (6)$$

where α and β are constants, assuming a constant catch per unit effort. The general patterns predicted by these analyses are similar to those in Figure 2B, D, with MacCall noting an inverse relationship between the apparent q and population abundance, and Fox noting a collapse of the fishery in plots of catch versus vessel-months, Figure 3. Both of these patterns may be the result of an inability to describe mathematically how the time available for searching increased as the population of sardines declined.

It is generally assumed that Atlantic menhaden have been overfished since the early sixties. Support for this conclusion was derived from the surplus-production work of Schaaf and Huntsman (1972), later updated by Schaaf (1975a). In both studies the available effort index (vessel-weeks) was modified in an attempt to correct for changes in fishing efficiency with time. Under the assumption of a constant q and lacking detailed information on vessel characteristics and catch, the authors adjusted effort by "multiplying the effort observed in each year by the relative change in q", using either 1965 (Schaaf and Huntsman) or 1971 (Schaaf 1975a) as a base year. The resulting pattern (Fig. 4A) strongly suggests that the fishery was operating on the descending arm of the catch-effort curve.

In another paper, Schaaf (1975b) observed an inverse relationship between his estimates of catchability coefficient and the population density, generating a pattern, like MacCall's (1976), similar to Figure 2D and at least partially explained by the lack of information on density-dependent searching time. However, Schaaf's apparent density-dependent estimate of q violates his early assumption of a constant q for use in standardizing the available effort data. The point is not trivial. Without this adjustment, the available effort data suggest that the Atlantic menhaden fishery is operating on the ascending arm of the catch-effort curve, Figure 4B.

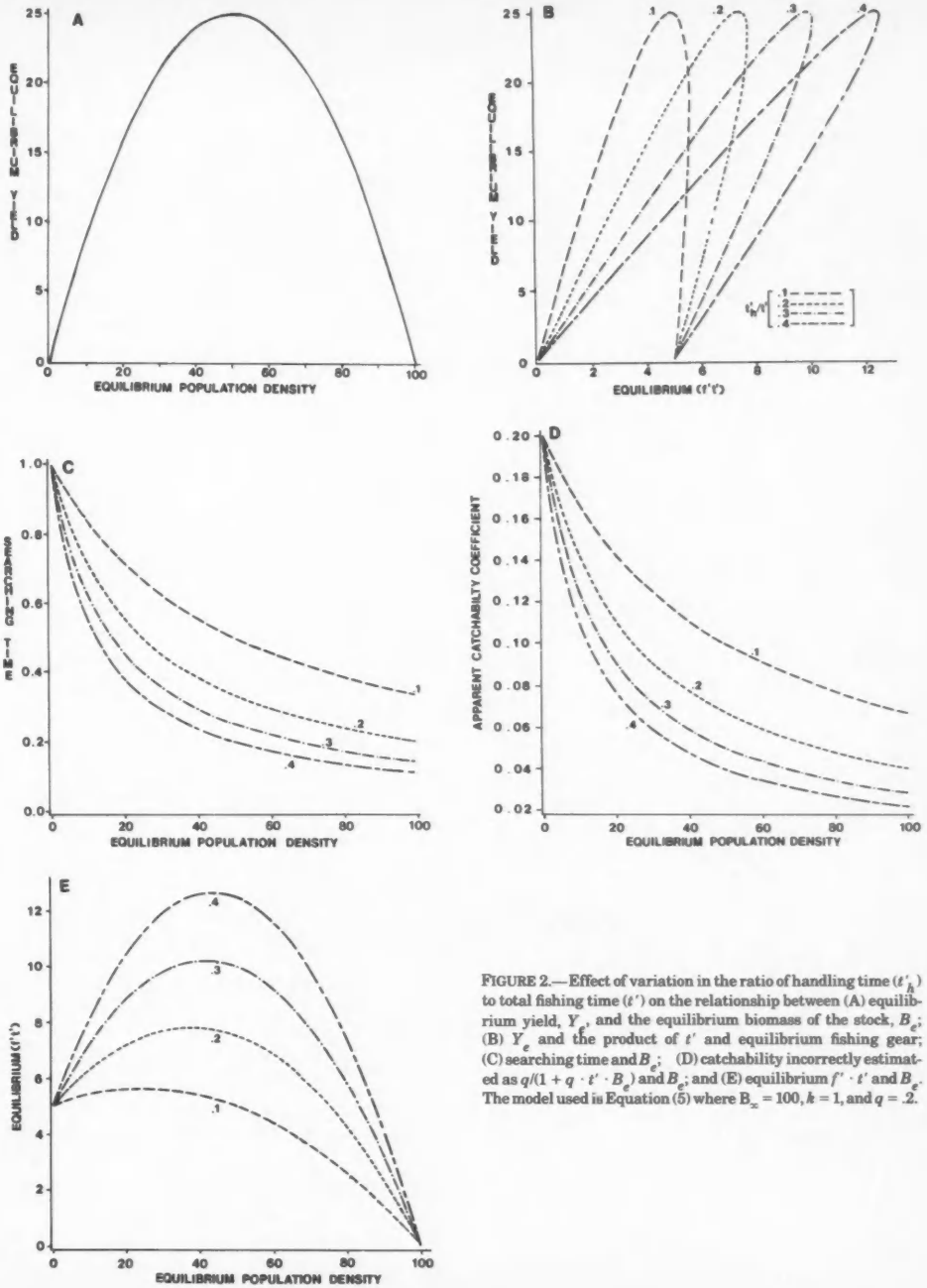

FIGURE 2.—Effect of variation in the ratio of handling time (t'_h) to total fishing time (t') on the relationship between (A) equilibrium yield, Y_e, and the equilibrium biomass of the stock, B_e; (B) Y_e and the product of t' and equilibrium fishing gear; (C) searching time and B_e; (D) catchability incorrectly estimated as $q/(1 + q \cdot t' \cdot B_e)$ and B_e; and (E) equilibrium $f' \cdot t'$ and B_e. The model used is Equation (5) where $B_\infty = 100$, $k = 1$, and $q = .2$.

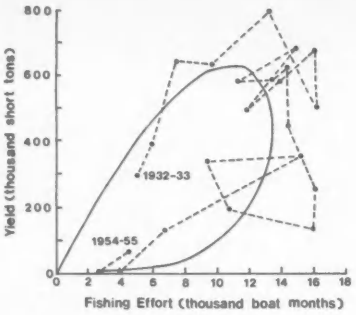

FIGURE 3.—Catch versus a nominal effort index for the California Pacific sardine fishery (after Fox 1974).

IMPLICATIONS

In this simple treatment, I have shown how some available estimates of fishing effort are inadequate to describe a fishery where searching time is stock-density dependent. More realistic models can be based upon an examination of detailed log-book data for inferences as to the relationships between searching time, stock abundance, prey and fleet distribution, and cooperation among the fleet. Hassel (1978) offers a comprehensive review of current approaches.

Even with better estimates of fishing effort a catastrophic collapse may be unavoidable because of parameters that cannot be measured or controlled (e.g., Clark and Manguel 1979). These estimates are important, however, in order to use surplus-production models for estimating the causes of such catastrophic collapses as that of the Pacific sardine fishery. Such estimates may also be necessary to suggest whether existing fisheries such as the Atlantic menhaden are actually being overfished.

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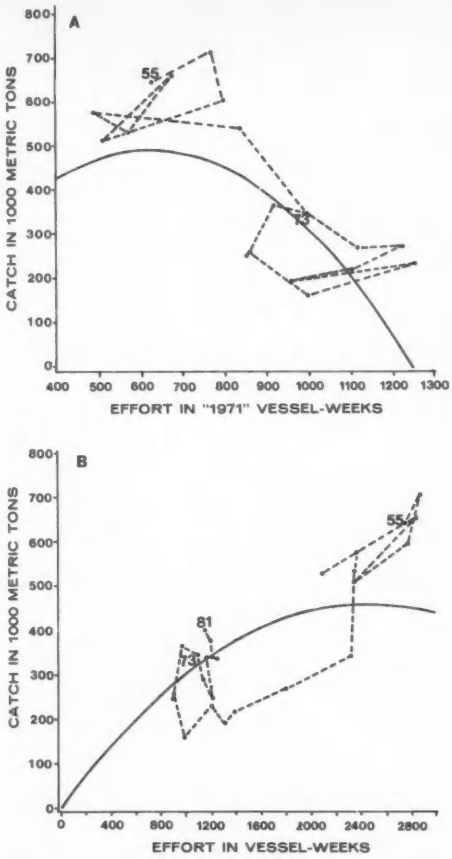

FIGURE 4.—Comparing the difference between fitting catch data for Atlantic menhaden when the effort is measured as (A) Schaaf's (1975a) 1971-vessel weeks and (B) vessel weeks. Curves were fit after the technique of Marchesseault et al. (1976).

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COMMUNITY AND TROPHIC ORGANIZATION OF NEKTON UTILIZING SHALLOW MARSH HABITATS, YORK RIVER, VIRGINIA[1]

STEPHEN M. SMITH,[2] JAMES G. HOFF,[2] STEVEN P. O'NEIL,[3] AND MICHAEL P. WEINSTEIN[3]

ABSTRACT

Nekton were collected by trawl and Wegener ring at each of two stations within tidal creeks and at adjacent shoal stations in the polyhaline and oligomesohaline zones of the York River estuary, Virginia. Species richness was significantly higher ($P < 0.05$) in Goalders Creek (oligomesohaline) compared with Blevins Creek (polyhaline) and may reflect the general absence of stenohaline marine "southern" taxa which seasonally occupy the tidal creeks of warm-temperate estuaries. In general, diversity was low in both creeks with dominance mainly shared by two species, *Leiostomus xanthurus* and *Anchoa mitchelli*. *Trinectes maculatus* also was abundant at the Goalders Creek shoal station, about 200 m outside of the creek mouth. A detailed analysis of the distribution of *L. xanthurus* indicated that after recruitment ceased, this species was largely resident in the creeks for several months, only emerging in the fall (October). Furthermore, emigration from Blevins Creek occurred earlier than at the upstream locality. Of the "transient" marine species encountered, *L. xanthurus* seemed to be the most tidal creek dependent. However, this may be due partly to the collection methodology employed.

Diet composition of six dominant species comprising >98% of the total number of individuals collected indicated that all were essentially trophic opportunists feeding on a wide variety of food items. Ontogenetic shifts in diet were also observed for the five most abundant species. Lack of dietary specialization and the consequently large degree of diet overlap in all species may reflect the nonlimiting nature of food abundance in the primary nurseries, however a seasonal change in relative fullness values may indicate periodic food scarcity.

The structural and functional role of shallow estuarine habitats has received increasing attention in the past few years. Although widely recognized as primary nurseries, two of these habitats, marshes and seagrass meadows, have only recently come under scrutiny in the lower Chesapeake Bay. Much of the impetus for these efforts was derived from priorities established by the Chesapeake Bay Program (Environmental Protection Agency 1979). As a result, areas covered with submerged aquatic vegetation (SAV) were investigated between 1977 and 1981. The role of SAV as primary nurseries, especially for blue crabs, *Callinectes sapidus*, was confirmed (Orth[4]). It was suggested (and, in some cases, demonstrated experimentally) that a principal function of vegetated habitats was that of predation refugium for the early life stages of many species (Heck and Thoman 1981; Lascara 1981; see also Nelson 1979 and Coen et al. 1981). Although seagrass meadows were contrasted with immediately adjacent unvegetated areas, their value compared with tidal salt marshes was not established.

To place the utilization of SAV and tidal creeks by the immature life stages of dominant species into better perspective, Weinstein and Brooks (1983) undertook a direct comparison of these areas along a contiguous marsh-seagrass ecosystem on the eastern shore of Virginia. Two results of their study were the observations that the dominant finfish in the area—spot, *Leiostomus xanthurus*—was nearly four times more abundant in the tidal creek throughout the study period, and that larger juvenile and adult blue crabs made nearly equal use of both habitats. A further outcome of this study was the obvious need for additional inventories of shallow waters of the lower Chesapeake Bay with regard to the relative value of different habitats to resident species.

For this reason we have extended our program to include a survey of habitat utilization by nekton occupying oligohaline and polyhaline tidal creeks

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of the York River estuary and have included a comparison of the tidal creeks with adjacent shoal areas (about 200 m outside of the tidal creek mouths). Along with data on community composition and structure, we have begun baseline studies of diet composition of dominant species. These aspects of community ecology of York River tidal marshes are reported herein.

STUDY AREA AND METHODS

The York River is one of six major tributaries which enter the Chesapeake Bay along its western shoreline. The narrow estuary covers about 208 km² and extends 46 km from Tue Marsh Light to West Point, Va. (Fig. 1). The upper portion of the York is characterized by broad, shallow flats and tidal creeks dominated by *Spartina* spp. along the shoreline. Upstream the river channel averages 8-9 m in depth, but broadens downstream and reaches a maximum depth of 18-23 m. The Guinea Marshes (Fig. 1) is a major *Spartina alterniflora*-dominated marsh system located near the estuary mouth. Much of the adjacent shallows in this region is carpeted with dense stands of eelgrass, *Zostera marina*, and widgeon grass, *Ruppia maritima*. Salinities are usually in the polyhaline range.

Two tidal creeks were selected for study. Goalders Creek (Fig. 1:location A) was located in the oligohaline-mesohaline zone just below the city of West Point. Blevins Creek (Fig. 1:location B), a part of the Guinea Marsh system, was situated in the polyhaline zone where salinities always exceeded 16‰. In each creek, one station was established as far upstream as possible, one near the creek mouth, and one about 200 m offshore. All collections were made monthly on consecutive days (March-October 1983), with sampling initiated as close to daytime high tides as possible. Miller and Dunn (1980) collected a greater proportion of fish with stomachs containing food at this time. Creek bottoms were of the mud-silt type and ranged from 1 to 1.5 m deep.

The primary collecting device utilized in this study was a 4.9 m otter trawl consisting of wings and body of 19 mm mesh and a liner of 6.3 mm mesh. This gear was towed for 2-min intervals at a speed of about 1.0 m/s at each station. In an earlier study at Guinea Marshes, Orth and Heck (1980) demonstrated that six hauls of the trawl were necessary in seagrass habitats to attain asymptotic returns on community information (as judged by several diversity indices). Because of the expectedly lower diversity in the tidal creeks (Weinstein and Brooks 1983), it was determined that four consecutive hauls at each tidal creek station would be sufficient to attain the same level of community information.

Ancillary collections were taken in the tidal creek with a modified Wegener ring (Wegener et al. 1973). The gear was used in depths <1 m, in the vicinity of the trawling stations. The side walls of the ring consisted of 1.5 mm woven netting, with the original design of the gear being changed to include a 305 mm "skirt" and chain attached to the

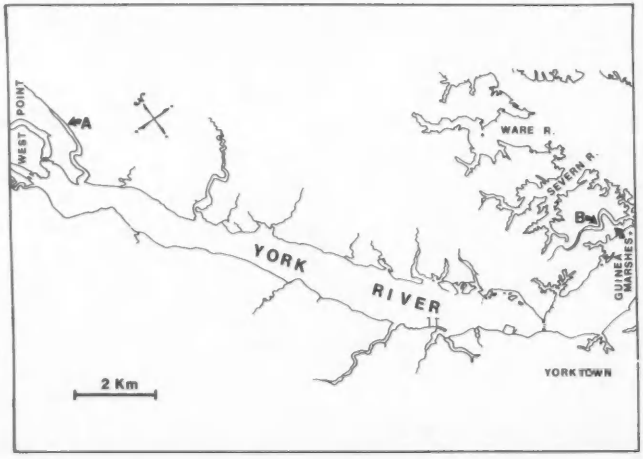

FIGURE 1.—Location of study areas in York River estuary, Va. Three permanent sampling stations were established—near the headwaters, at the mouth, and 200 m offshore of an oligo-mesohaline (A = Goalders Creek) and polyhaline (B = Blevins Creek) tidal creeks.

leadline hoop which helped fill contours along the bottom. Samples were obtained by tossing the ring from shore and then applying rotenone at a 30 ppb concentration within the confines of the net (Weinstein and Brooks 1983). Stricken fishes were then captured with dip net or swept off the bottom.

Fishes were sorted into 20 mm (or less) size classes and up to 20 randomly selected individuals from each class used for trophic analyses. Stomach fullness was recorded as a relative fullness index (RFI) value (Hyslop 1980). Stomach contents were subsequently analyzed using a modified Carr and Adams (1972) sieve fractionation technique. Total dry weights for each sieve fraction were then obtained and proportioned among the prey taxa identified from a five drop subsample taken before drying. On the assumption that particles of equal size have approximately the same weight, this method agglomerates food particles of roughly the same size.

The Carr and Adams technique provided rapid, accurate identification of food items for a large number of stomachs and has been used with success by several investigators (Sheridan 1979; Sheridan and Livingston 1979; Stoner 1980; Livingston 1982). A useful modification employed in this study was the application of a low pressure stream of compressed air delivered through a Pasteur pipette which greatly aided in removing food particles adhering to the finer screens of the sieves.

Numerical classification analysis used here is similar to the procedures employed by Weinstein (1979) and Weinstein and Brooks (1983). Briefly, marsh creek communities and trophic ecology of dominant species were compared by classification methods using "normal" and "inverse" classification (Clifford and Stephenson 1975). The former method groups sites (or predators) by their species (or prey taxon) attributes; while inverse classification (used only for community analysis purposes here) groups species according to their site of occurrence (i.e., the sites become the attributes of the species). Similarity between sites (or predators) was calculated as the complement of the Canberra metric index:

$$[1/n]\left[\sum_{1}^{N}\right]\left|x_{1j} - x_{2j}\right|/(x_{1j} + x_{2j}) \qquad (1)$$

where n = number of attributes, and x_{1j} and x_{2j} are the values of the jth attribute for any pair of entities. The merits of the Canberra metric index have been discussed by Clifford and Stephenson (1975).

Separate matrices were constructed for each comparison from untransformed, pooled monthly data and clustered by the unweighted pair, group-average strategy (Clifford and Stephenson 1975). Species occurring at only one station (singletons) were eliminated prior to the community analyses. Combined trawl and Wegener ring data were used separately in these procedures. Dendrograms for site and species dissimilarity (community analyses) were constructed and cross-tabulated in a two-way coincidence table.

All nekton were preserved in 10% buffered Formalin[5]. Standard length (SL, carapace width for blue crabs) was recorded for all taxa. Up to 30 individuals/species were measured from each collection, subsampling for lengths was employed when sorted collections contained more than 30 individuals of a given species. Prior to each collection, temperature and salinity were recorded with an immersion thermometer and a temperature-compensated refractometer.

RESULTS

Abundance and Seasonality

Only two species—spot and the bay anchovy, *Anchoa mitchelli*—comprised >90% of the total number of individuals captured at Blevins Creek and adjacent shoals. Using this same criterion, upstream densities were more equitably distributed with four species in the creek and six on the shoal sharing dominance (Table 1). Blue crabs; white perch, *Morone americana*; and the hogchoker, *Trinectes maculatus*, were in this group in Goalders Creek, while in late summer and fall the Atlantic croaker, *Micropogonias undulatus*, and the weakfish, *Cynoscion regalis*, were also abundant at the shoal station (Table 1).

Species richness (S) was also greater in all months in the Goalders Creek system compared with the polyhaline Blevins Creek (Fig. 2) and was significantly greater for the entire study period (Wilcoxon sign-ranks test; $P < 0.05$). No apparent trend, however, was evident in the number of individuals captured at each locality (Fig. 2), except that peak catches of two dominant species, spot and bay anchovy, were greater in Blevins Creek and resulted in the large disparity in catches in

[5]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Pooled species abundance and percent composition for all trawl collections, York River estuary, Va. N = number of individuals.

Species	N	%
Goalders Creek upstream		
Leiostomus xanthurus	709	[1]70.69
Callinectes sapidus	83	[1]8.27
Anchoa mitchilli	69	[1]6.88
Morone americana	48	[1]4.79
Alosa aestivalis	35	3.49
Morone saxatilis	27	2.69
Ictalurus catus	25	2.49
Brevoortia tyrannus	3	0.30
Pomatomus saltatrix	1	0.10
Peprilus alepidotus	1	0.10
Anguilla rostrata	1	0.10
Trinectes maculatus	1	0.10
Total	1,003	100.00
Blevins Creek upstream		
Leiostomus xanthurus	1,301	[1]46.51
Anchoa mitchilli	1,248	[1]44.62
Callinectes sapidus	162	5.79
Trinectes maculatus	35	1.25
Brevoortia tyrannus	23	0.82
Menidia menidia	17	0.61
Fundulus heteroclitus	5	0.18
Gobiosoma bosci	3	0.11
Cynoscion regalis	1	0.04
Morone americana	1	0.04
Microgobius thalassinus	1	0.03
Total	2,797	100.00

Species	N	%
Goalders Creek downstream		
Leiostomus xanthurus	1,646	[1]60.09
Trinectes maculatus	385	[1]14.05
Anchoa mitchilli	373	[1]13.62
Callinectes sapidus	144	[1]5.26
Ictalurus catus	75	2.74
Morone americana	57	2.08
Brevoortia tyrannus	17	0.62
Cynoscion regalis	16	0.58
Morone saxatilis	8	0.29
Paralichthys dentatus	3	0.11
Micropogonias undulatus	3	0.11
Alosa aestivalis	3	0.11
Opsanus tau	3	0.11
Pomatomus saltatrix	2	0.07
Peprilus alepidotus	1	0.04
Alosa sapidissima	1	0.04
Anguilla rostrata	1	0.04
Syngnathus fuscus	1	0.04
Total	2,739	100.00
Blevins Creek downstream		
Leiostomus xanthurus	1,501	[1]73.69
Anchoa mitchilli	414	[1]20.32
Callinectes sapidus	103	5.05
Paralichthys dentatus	6	0.30
Menidia menidia	5	0.24
Gobiosoma bosci	2	0.10
Trinectes maculatus	2	0.10
Cobiesox strumosus	2	0.10
Peprilus triacantus	1	0.05
Microgobius thalassinus	1	0.05
Total	2,037	100.00

Species	N	%
Goalders Creek shoal		
Trinectes maculatus	1,439	[1]50.31
Leiostomus xanthurus	412	[1]14.40
Anchoa mitchilli	310	[1]10.84
Callinectes sapidus	308	[1]10.77
Micropogonias undulatus	91	[1]3.18
Cynoscion regalis	77	[1]2.69
Ictalurus catus	59	2.06
Morone americana	57	1.99
Anchoa hepsetus	33	1.15
Opsanus tau	28	0.98
Ophidion marginata	13	0.45
Paralichthys dentatus	12	0.42
Anguilla rostrata	8	0.28
Morone saxatilis	5	0.18
Menticirrhus saxatilis	3	0.11
Pomatomus saltatrix	2	0.07
Peprilus alepidotus	1	0.04
Brevoortia tyrannus	1	0.04
Gobiosoma bosci	1	0.04
Total	2,860	100.00
Blevins Creek shoal		
Leiostomus xanthurus	1,935	[1]80.03
Anchoa mitchilli	385	[1]15.92
Callinectes sapidus	49	2.03
Trinectes maculatus	10	0.42
Bairdiella chrysoura	10	0.42
Paralichthys dentatus	6	0.25
Opsanus tau	4	0.17
Micropogonias undulatus	3	0.12
Stenotomus chrysops	2	0.08
Anchoa hepsetus	2	0.08
Syngnathus fuscus	2	0.08
Gobiosoma bosci	2	0.08
Menidia menidia	2	0.08
Synodus foetens	2	0.08
Centropristis striata	1	0.04
Rachycentron canadum	1	0.04
Brevoortia tyrannus	1	0.04
Urophycis regia	1	0.04
Total	2,418	100.00

[1]Species comprising >90% of the total number of individuals.

May and July. Except for the spike seen in Figure 2, resultant from a large influx of bay anchovy into Blevins Creek in July, combined catches of all other taxa were at a minimum for the summer months (June-August) coincident with peak summer temperatures.

Seasonal abundance of the more common species was typically associated with recruitment of young-of-year individuals into the tidal creeks and adjacent shoals. Young spot dominated in both creeks but were subsequently replaced by post-larval and juvenile bay anchovy (July), and thereafter at Goalders Creek by hogchoker (August), weakfish (August-September), and Atlantic croaker (October). In addition, white catfish, *Ictalurus catus*, and white perch were frequently captured in the Goalders Creek vicinity during early spring when salinities were at their lowest recorded levels. Because of the overall seasonal abundance, it was possible to examine spatial and temporal distributions of spot in greater detail (Fig. 3, Table 2). As expected, spot were more abundant outside of the creeks very early in recruitment; but by June had established a greater degree of residency within the creeks compared with the adjacent shoals. This pattern of large creek to shoal abundance ratios (Fig. 3) continued (with a single exception) until October when spot emerged from Blevins Creek. Note, however, that at the termination of the sampling program, this emigration had not taken place upstream. Similar

TABLE 2.—Relative abundance of *Leiostomus xanthurus* at tidal creek stations, York River estuary.

Location	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.
Goalders Creek								
Upstream	0	1	401	85	51	58	68	45
Downstream	0	52	624	318	236	172	93	151
Blevins Creek								
Upstream	0	19	493	326	292	60	105	6
Downstream	0	18	586	337	102	150	221	87

patterns of earlier downstream emigration were observed during 1976-78 in the Cape Fear estuary, N.C. (Weinstein and Walters 1981; Weinstein pers. obs.), the cause of which remains unexplained. It is evident from Table 2 that spot may have been more restricted in their upsteam movement in Goalders Creek where salinities averaged about 2‰ lower at the upsteam station than at the creek mouth. The ratio of upstream to downstream station catch was twice as high at Blevins Creek, supporting this pattern. Other species which seem to prefer a specific portion of the tidal creek to shoal habitat gradient included hogchoker, weakfish, and Atlantic croaker which had creek-to-shoal ratios (over all months) of 0.13, 0.10, and 0.02, respectively. Moreover, these species were far more abundant at upstream sites (Table 1).

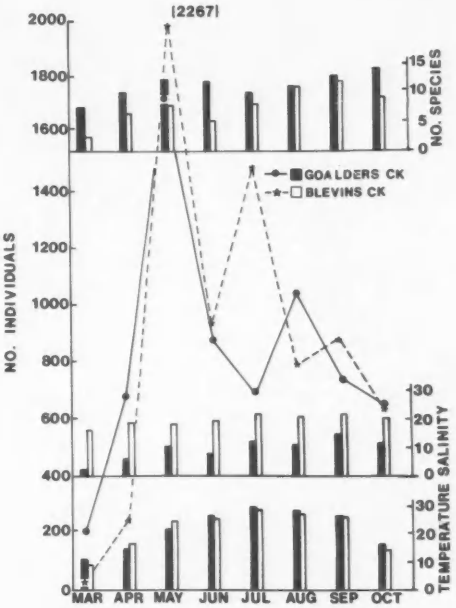

FIGURE 2.—Total numbers of individuals and species captured in monthly tidal creek collections. Temperatures and salinities are mean values recorded at each creek in each month.

Community Composition

A two-way coincidence table, using a similarity value of 0.200 to define clusters (Clifford and Stephenson 1975), was constructed in order to summarize species and site relationships for pooled monthly collections at each station (Table 3). Included in this analysis are samples collected with the Wegener ring, a gear which was expected to be more successful in collecting both cryptic species (e.g., Gobiidae) and shore-zone taxa (e.g., cyprinodonts [Cyprinodontidae] and silverside [Atherinidae]). It should be pointed out, however, that any comparisons between the Wegener ring and trawl samples are qualitative since no attempt was made to compare gear selectivity, efficiency, and area encompassed by a unit effort for each sampling device (Weinstein and Brooks 1983).

Species group IV (Table 3) was generally the most ubiquitously distributed assemblage over the range of environmental factors (particularly

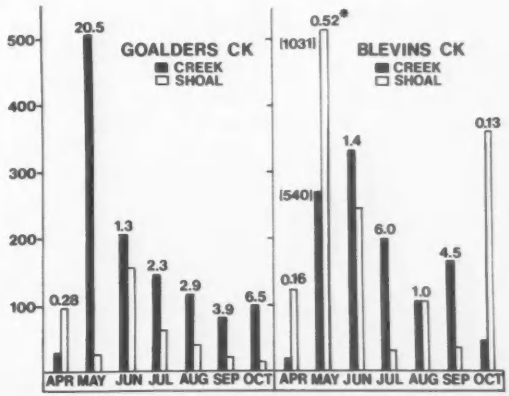

FIGURE 3.—Relative densities of *Leiostomus xanthurus* at tidal creek (values shown are monthly means for both creek stations) and shoal sampling localities. May values for Blevins Creek are drawn to half-scale. Values appearing above histograms are ratios of creek to shoal densities.

TABLE 3.—Two-way coincidence table comparing stations (Groups A-D) and species (groups I-VI) associations at York River estuary sites. Clustering by unweighted-pair group-average; similarity index = Camberra metric, all data $\log_{10}(x + 1)$ transformed, single station occurrences dropped. G = Goalders Creek, B = Blevins Creek, U = upstream, D = downstream, S = shoal stations, W = Wegener ring samples.

		A			B			C			D
Group	Species	GU	GD	GS	BU	BD	BS	GUW	BDW	BUW	GDW
I	*Paralichthys dentatus*		3	12		6	6				1
	Micropogonias undulatus		3	91			3				
	Opsanus tau		3	28			4				
	Anchoa hepsetus			33			2				
	Cynoscion regalis		16	77	1						
	Syngnathus fuscus			1			2	1			
II	*Pomatomus saltatrix*	1	2	2							
	Peprilus alepidotus	1	1	1							
	Anguilla rostrata	1	1	8							
	Morone saxatilis	27	8	5							
	Ictalurus catus	24	75	59							1
	Brevoortia tyrannus	3	17	1	23		1				7
III	*Alosa aestivalis*	35	3					1	1		5
	Fundulus heteroclitus				5			1	3	23	1
	Menidia beryllina							3	6		3
IV	*Morone americana*	48	57	57	1			2		1	10
	Leiostomus xanthurus	709	1,646	412	1,301	1,501	1,935	9	14	14	3
	Anchoa mitchilli	69	373	310	1,248	414	385	3		4	32
	Trinectes maculatus	1	385	1,439	35	2	10	1			
	Callinectes sapidus	83	144	308	162	103	49				
	Gobiosoma bosci			1	3	2	2	2	13	4	106
	Menidia menidia				17	5	2				24
V	*Fundulus majalis*									2	1
VI	Microgobius thalassinus				1	1					

salinity) examined. Nonetheless, within this group were several species which displayed area-specific distributions, in either relative numbers or presence/absence in a given creek system. Examples of the former include the hogchoker and bay anchovy and of the latter, white perch, which was far more prevalent upstream. The Goalders Creek nekton community was also dominated by members of groups I and II, whose members were rare or absent at downstream localities. Remaining species were generally not captured in sufficient numbers to depict their role in defining community structure in each area.

Trophic Analysis

Six species (Fig. 4) were sufficiently abundant in time and space to allow a comparative trophic analysis to be undertaken. Collectively, they exceeded 98% of the total number of individuals captured during this study. Prey taxa were defined on the basis of 39 categories (Table 4). All but two—miscellaneous (MISC) and unidentified (UID)—were mutually exclusive. These two did not exceed 17% of the total diet composition of any one species and were generally much lower than this amount. The dietary relationships of these six species are summarized across all sampling strata by the dendrograms appearing in Figure 4. With the exception of summer flounder, *Paralicthys dentatus*, sufficient numbers of individuals were captured to also allow partitioning by size classes. Such ontogenetic summaries are shown in Figure 5.

Although more than 2,600 specimens were examined for diet composition, sample sizes were not sufficient in the first year of the study to examine details of seasonal nor spatial food utilization in all species except spot (O'Neil 1983). In addition, several species were only abundant in a restricted area (Table 1) or attained peak abundance in a relatively narrow time frame, precluding dietary comparison of dominant species (Fig. 6).

Diet overlap was greatest between white perch and hogchoker (Fig. 4). Dietary items shared by these species included clam siphons, *Leoptochirus plumulosus*, and other gammarid amphipods. Both predators were generally habitat-specific, with young-of-year white perch more abundant in the creeks and hogchoker prevalent on the river shoals (Table 1). Largely because of fish (TEL) included in the diet of larger individuals, white catfish displayed somewhat less overlap in its diet compared with the former species, but because of its partial piscivorous habits shared this similarity with the major fish predator captured in our trawl samples—the summer flounder. Both small summer flounder and white perch (<61 mm) also consumed substantial quantities of the mysid shrimp *Neomysis americana*.

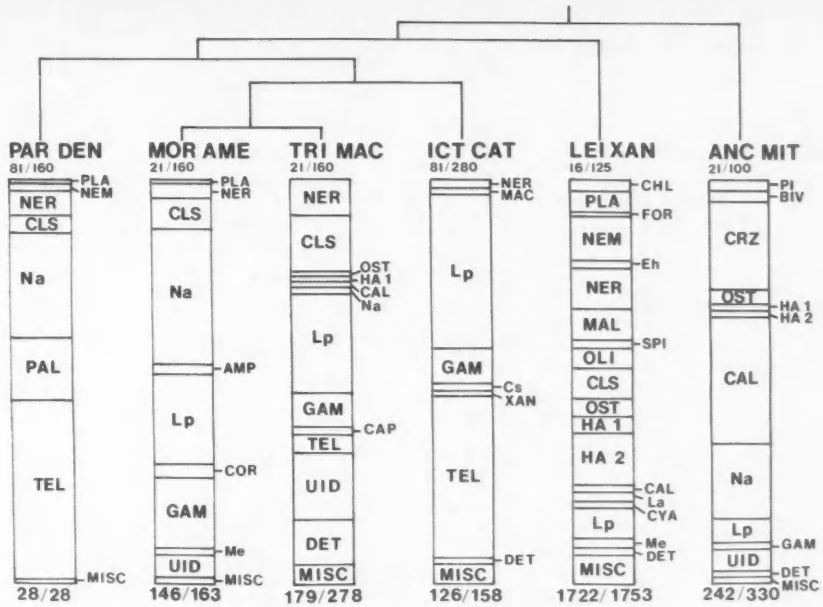

FIGURE 4.—Trophic comparisons among dominant predators (those comprising >98% of the total number of individuals captured), pooled across all sampling strata. PAR DEN = *Paralichthys dentatus*; MOR AME = *Morone americana*; TRI MAC = *Trinectes maculatus*; ICT CAT = *Ictalurus catus*; LEI XAN = *Leiostomus xanthurus*; ANC MIT = *Anchoa mitchilli*. Ratios appearing below histograms represent stomachs with food as a proportion of total stomachs. Values above histograms are size ranges (standard lengths). Diet composition was compared using Canberra metric and unweighted-pair group-average clustering strategy, data untransformed. Prey designations are defined in Table 4.

TABLE 4.—Prey categories used for trophic comparisons. All but unidentified (UID) and miscellaneous (MISC) are mutually exclusive feeding categories.

AMP	Amphipoda	La	*Leucon americanus*
BIV	Bivalves	Lp	*Leptocheirus plumulosus*
BRA	Branchipoda	MAC	*Macoma* sp.
CAL	Calanoids	MAL	Maldanidae
CAP	Caprellidae	Me	*Monoculodes edwardsi*
CLS	Clam siphons	MISC	Miscellaneous
CHI	Chironomidae	Na	*Neomysis americana*
CHL	Chlorophyta	NEM	Nematoda
COR	Corophiidae	NER	Nereidae
Crs	*Crangon septemspinosa*	OLI	Oligochaeta
CRZ	Crab zoea	OST	Ostracods
Cs	*Callinectes sapidus*	PAL	Palaemonidae
CYA	Cyathura	PI	Polydora ligni
DET	Detritus	PLA	Plant matter
Eh	*Eteone heteropoda*	POL	Polychaeta
Et	*Edotea tribola*	SPI	Spionidae
FOR	Foraminifera	TEL	Teleostei
GAM	Gammaridae	UID	Unidentified remains
HA1	Harpacticoid 1	XAN	Xanthidae
HA2	Harpacticoid 2		

Among the six species examined, spot and bay anchovy displayed the least dietary overlap, with the former exhibiting the greatest dietary diversity (consisting mainly of benthic prey items), and the latter including a greater percentage of planktonic food items in its diet. However, the large variety of prey items consumed by all species indicates that each is a trophic opportunist (Darnell 1958, 1961; Carr and Adams 1973; Sheridan and Livingston 1979; Livingston 1982).

Ontogenetic shifts in diet were evident for each of the species examined (Fig. 5). In spot, dietary importance of calanoid copepods declined in fish >20 mm SL, while harpacticoid copepods increased in importance in fish 21-80 mm SL. Concurrently, the percentage of various polychaetes and gammarid amphipods slowly increased in their diet. Nematodes also became less important with increasing size. Interestingly, spot stomachs at all sizes contained clam siphons and maldanid tails, indicating that specific parts of larger prey were important dietary items.

Ostracods and crab zoea were abundant food items for small (<21 mm SL) bay anchovy; larger

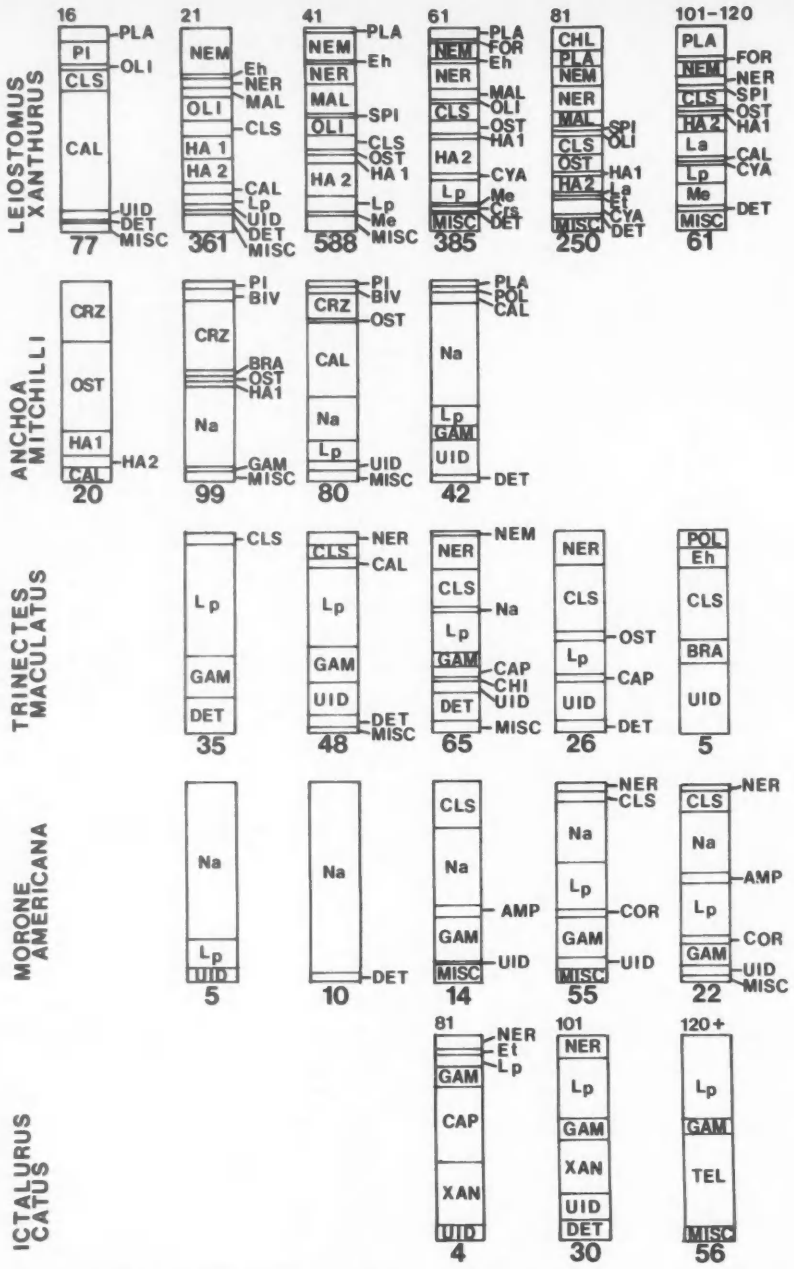

FIGURE 5.—Ontogenetic comparisons in diet among the five most dominant species captured in this study. Sample size (stomachs with food) appear below histograms, size increment (standard length) above. Prey designations are defined in Table 4.

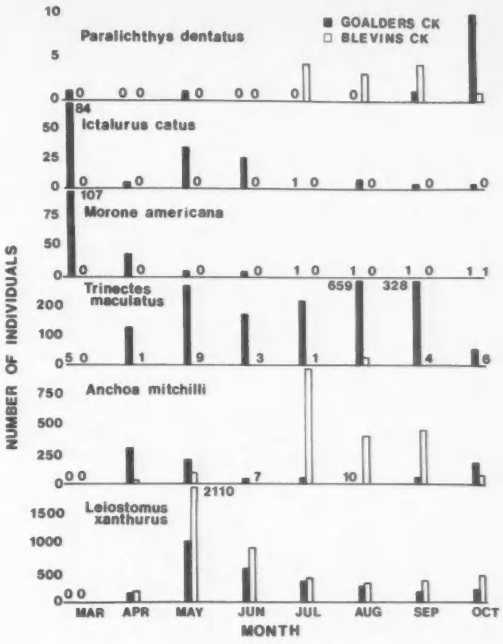

FIGURE 6.—Seasonality of selected taxa at tidal creek and shoal stations, York River estuary, Va. Numbers on x axis are sample sizes too small to plot.

individuals incorporated more *Neomysis americana*, calanoid copepods, and gammaridean amphipods into their diet. In hogchokers, however, gammarids predominated in smaller individuals, <61 mm SL, but with increasing size became somewhat less important and were replaced by nereid polychaetes and clam siphons. Hogchokers had the highest proportion of unidentified remains (UID) of any predator examined due to the high level of maceration characteristic of this species.

Neomysis americana was clearly the dominant prey item of small (<60 mm SL) white perch, but became less important in the diets of larger individuals which fed increasingly on gammarid amphipods and clam siphons. White catfish <120 mm SL also fed conspicuously on amphipods but, uniquely among the predators examined, also fed upon xanthid crabs, and at larger sizes incorporated a substantial proportion of fishes into their diet.

Relative fullness indices displayed varying trends on a species-specific basis (Table 5). Values declined in the later part of the study for white perch and white catfish, whereas no apparent trends were observed for other species.

TABLE 5.—Monthly relative fullness index (RFI) for six dominant fishes in the York River estuary, Va. Values are means for all individuals examined.

Species	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.
Anchoa mitchilli		0.66	2.73	1.60	2.16	2.72	2.43	1.03
Ictalurus catus	2.53	2.20	1.84	1.50		1.19	1.74	1.00
Leiostomus xanthurus		2.45	2.45	2.62	2.59	2.77	2.51	1.98
Morone americana	2.65	1.59	1.14	1.00		1.00		0.50
Paralichthys dentatus	2.60				3.33	2.50	3.50	4.00
Trinectes maculatus		1.82	1.91	1.45	1.47	1.60	0.88	1.30

DISCUSSION

Species Composition and Abundance

Along with other recent studies of shallow-water nekton (Orth and Heck 1980; Weinstein and Brooks 1983; Heck and Thoman 1984), the present effort provides additional information on the use of inshore habitats of the lower Chesapeake Bay. A striking characteristic of the marsh nekton community in the lower Chesapeake Bay is the generally low diversity of the constituent fauna and the high level of dominance of only a few species. On both the eastern shore of Virginia (Delmarva Peninsula) (Weinstein and Brooks 1983) and in the

York River estuary, no more than two species comprised >90% of the total number of individuals captured at polyhaline tidal creek stations. On the average, spot comprised 71.8% of this total. Only in the oligomesohaline Goulders Creek was species dominance shared by more than two species (Table 1), but once again, spot predominated with 65.4% of the total. By comparison, Hackney et al. (1976) reported a mean of seven species totaling >90.0% at four trawl stations in their study of a mesopolyhaline tidal creek in Georgia, while in several studies in South and North Carolina (Cain and Dean 1976; Bozeman and Dean 1980; Weinstein et al. 1980) three to nine species ($\bar{x} = 7$) comprised this total. Species richness was significantly greater in Goalders Creek than in the polyhaline Blevins Creek system. This is somewhat surprising since previous studies have often shown that diversity decreases for both fishes and invertebrates in the upstream direction (Dahlberg 1972; Boesch 1977; Gainey and Greenberg 1977; Weinstein et al. 1980). The absence or scarcity of stenohaline marine species derived largely from the seasonally abundant southern Carolinian ichthyofauna may partially explain this difference in the York River estuary. In North Carolina, for example, these taxa increased species richness in polyhaline tidal creeks, especially near the estuary mouth (Weinstein 1979; Weinstein et al. 1980). Also present in estuaries below the Chesapeake Bay are species with warm-temperate affinities which share dominance with spot and bay anchovy, including *Mugil cephalus, M. curema, Lagodon rhomboides, Paralichthys lethostigma, Bairdiella chrysura*, and the brown shrimp, *Penaeus aztecus*. These species are much less common in the Chesapeake Bay.

Another noteworthy finding is that species replacement does not occur from regional and northerly taxa. For example, *Ophidion marginata, Stenotomus chrysops, Urophysis regia*, and *Centropristis striata* were only rarely encountered in our studies (Weinstein and Brooks 1983). In the present investigation, these species were restricted to shoal stations outside of the tidal creek mouths (Table 1). Thus, there appears to be an underutilization of shallow nursery habitats by transient marine fishes in the Chesapeake Bay compared with the lower latitude estuaries (for more detailed discussion see Weinstein and Brooks 1983 and Heck and Thoman 1984). This difference is perhaps due partly to the unique location of the Chesapeake Bay in the transition zone between faunal provinces (Briggs 1974) with neither taxonomic group able to adapt fully to conditions (primarily temperature regimes and their variance?) associated with this transition zone. The recent geological and evolutionary history of northern estuaries, including the Chesapeake Bay (Shubel and Hirschberg 1978), may also play a role in determining the degree of estuarine dependency of local faunas.

A unique aspect of this study was the opportunity to compare utilization of the tidal creeks with adjacent shoal areas. Previously, these comparisons had to be made among collections with different gears (and their associated selectivity and efficiency) or in different years or by different investigators (Chao and Musick 1977; Markle 1976). The results for spot are of interest because of the general dominance of this species in many estuaries along the Atlantic and Gulf coasts.

Recently, Weinstein and Walters (1981), Weinstein and Brooks (1983), and Weinstein (1983) described the importance of marshes, specifically tidal creeks, to this species and the relationship between productivity and energy export via several fish vectors—from the marshes ultimately to the marine environment (Weinstein 1981). Spot were recruited into upstream marshes of the York River estuary earlier than to downriver sites and tended to remain there longer (Fig. 3). Once recruited into the marshes (by June) spot reside here until fall, when they emigrated into deeper water, and finally (for most individuals) return to the marine environment. As expected, however, there is an upstream limit to utilization in oligohaline tidal creeks where we found densities of spot decreased (Table 2) as salinities became more variable (approaching 0‰) and where temperature regimes became more unstable (Hackney et al. 1976). Whether the lower abundance of spot outside of the creeks is due to differential mortality and/or habitat selection remains unknown. Other taxa, e.g., young-of-year Atlantic croaker, weakfish, and hogchoker, apparently prefer the shoals and generally deeper water. There is little question that they are more abundant outside of the marshes (Chao and Musick 1977; Orth and Heck 1980; Weinstein and Brooks 1983; Middleton, unpubl. data). If, as many would argue, predation is a major regulator of local abundance and ultimately community structure, what protection would the homogenous, relatively unstructured shoals and flats afford these species? Considering the apparent physical and behavioral similarities, as well as recruitment dynamics between spot and Atlantic croaker, there does not seem to be any

significant adaptive feature of the latter that would provide better survivorship in open waters (at least with regard to predation). Just how this species and others minimize the effects of predation in open waters is an important research question for the future.

Trophic Comparisons

The six species examined in detail are clearly trophic opportunists and overlap in many food categories. In addition, each goes through distinct ontogenetic stages in feeding which include significant shifts in the portions of the water column searched. The prey taxa have been categorized by Darnell (1961), Qasim (1972), and Chao and Musick (1977) according to their vertical occurrence in the water column from open waters to the bottom: fishes, macrozooplankton (e.g., *Neomysis americana*), microzooplankton (e.g., calanoid copepods), epibenthos (e.g., harpacticord copepods), infauna, and organic matter. At sizes <21 mm SL all five of the species examined apparently spent considerable periods foraging in the water column. Between 21 and 40 mm SL several species continued to feed on "pelagic" prey, although by this size the transition to benthic feeding was nearly complete in spot and hogchoker.

Whether resource partitioning or dietary specialization (Chao and Musick 1977) occurs in these taxa as a means of reducing interspecific interactions is a matter of speculation. Without question, there are differences in feeding localities of the fishes examined—e.g., white perch and white catfish are generally restricted to oligohaline habitats, while Atlantic croaker and hogchoker are more abundant on the shoals. Also noted are differences in seasonal abundance (Fig. 6), size related feeding distributions reflecting ontogenetic shifts (Fig. 5), morphological differences among predators (Chao and Musick 1977), etc. But whether or not any of these traits reflect past or present competitive pressures remains unknown. Food that is generally limiting for several of these species and others is currently an area of controversy. Currin et al. (in press) have suggested that predation, not resources, limits production rates of spot and Atlantic croaker in shallow marsh embayments in Albermarle Sound, N.C. In contrast, Weisberg and Lotrich (1980) found that growth rates of the mummichog, *Fundulus heteroclitus*, could be altered by manipulating fish density. Increased growth rates were also demonstrated with food enrichment experiments in subtidal areas. Similar findings were reported by Miklas and Reed (in press) for *F. heteroclitus* populations in a tidal tributary of the Rhode River, Del. Our own findings of a seasonal decline in relative fullness index values in several species, along with a parallel decline in benthic biomass (T. Fredette[6]), tend to support the possibility of periodic food scarcity.

Trophic opportunism has often been cited in studies of estuarine fishes (Darnell 1958, 1961; Livingston 1982). Several investigators have pointed to the importance of omnivorous and ontogenetic progressions in feeding stages (Sheridan 1979; Stoner 1980; Livingston 1982) as obscuring distinct trophic relationships in nektonic food webs. Along with these difficulties are problems associated with the "snapshot" view often gained of the system. Numerically abundant species are likely to play the major role in conversion and production of organic materials in estuaries (and are, therefore, mainly responsible for the construct of food webs and energy flow therein), yet the identification of these species often comes from the sampling program itself.

Thus, although the dominant species in this study, spot, is undoubtedly important in this regard, the selective nature of our sampling effort does not allow us to place this importance in proper perspective. It is probable that dominance, expressed in numbers and/or biomass of those species captured in this study, is shared and sometimes surpassed by other local species not sampled quantitatively by this program. These include young-of-year bluefish, *Pomatomus saltatrix*; various cyprinodonts, especially *F. heteroclitus*; anchovies; and silversides. On an estuary-wide basis, we also do not completely "track" species distributions in time and space (Purvis 1976) so that our already distorted view of local habitats cannot easily be extrapolated to system-wide considerations. Such difficulties occur in most studies and must be recognized and eventually accounted for in considerations of fish community ecology in estuaries.

SUMMARY

Tidal creeks of the York River estuary were characterized by distinct nekton communities displaying low diversity and dominated by relatively

[6]T. F. Fredette, Marine Scientist, Department of the Army/Corps of Engineers, P.O. Box 631, Vicksburg, MS 39189, pers. commun. September 1982.

few taxa. Of the many transient marine species (Weinstein 1979; Weinstein et al. 1980) that utilize marsh creeks along the Atlantic coast, only the spot, *Leiostomus xanthurus*, seemed to actively select this habitat. Within creeks there also was an apparent upstream limit in abundance of this species at low salinities. Although not captured quantitatively in this study, Atlantic menhaden, *Brevortia tyrannus*, were often observed in large numbers in the creeks, especially upstream. Other species, particularly Atlantic croaker, weakfish, and hogchoker were captured in greater numbers in low salinity shoal waters (<5 m) adjacent to marshes. Compared with the polyhaline marshes and shoals, stations sampled upstream in oligomesohaline waters were more diverse and had a larger variety of taxa apparently utilizing this area as a primary nursery habitat. In addition to the species mentioned above, white perch; striped bass, *Morone saxatilis*; and white catfish were seasonally present as young-of-year in the area.

Dietary composition of the six species examined in detail reflected that of trophic opportunism, with maximum dietary diversity displayed by spot. Ontogenetic progressions in diet also were observed in all species. Two species, summer flounder and white catfish, were piscivorous at larger sizes, feeding mainly on *Anchoa* spp. The apparent absence of specialization in any of these predators may reflect the general adequacy of food supplies in the primary nurseries.

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DISTRIBUTION, ABUNDANCE, AND GROWTH OF JUVENILE DUNGENESS CRABS, *CANCER MAGISTER*, IN GRAYS HARBOR ESTUARY, WASHINGTON[1]

BRADLEY G. STEVENS[2] AND DAVID A. ARMSTRONG[3]

ABSTRACT

Dungeness crabs, *Cancer magister*, were collected biweekly or monthly from May 1980 to July 1981 in Grays Harbor, Washington. Age of each crab was estimated from width-frequency analyses, and the population density and growth rate were monitored for each age class over the 14-month period. In April 1980 and 1981, crabs entered the estuary either as megalops larvae that metamorphosed to first instar postlarvae or directly as first instars. Intertidal mudflats with beds of eelgrass (*Zostera* spp.) were important habitats for the first few postlarval stages. Some crabs may have emigrated from the estuary during their second year of life, whereas others dispersed throughout the estuary and appeared to emigrate at sexual maturity (about 2 years). No gravid females were ever found in the bay. Population size was estimated to range from 3.3 million crabs (winter) to 39.0 million crabs (summer); 74% of the summer population were early instars. Growth of early instars was rapid and resulted in a 282-fold increase in dry weight from May to September, but little growth occurred during the remainder of the year. Based on summer population abundance, it is estimated that this estuary could account for a substantial portion of recruitment to the offshore commercial fisheries.

The biology of the Dungeness crab, *Cancer magister*, has been studied by numerous investigators for several decades (Weymouth and MacKay 1936; MacKay 1942) because of its importance to commercial fisheries and its position as a benthic predator in estuaries and offshore communities (Gotshall 1977; California Department of Fish and Game 1981). Previous studies of *C. magister* biology have been conducted largely along the open coast (MacKay 1942; Cleaver 1949; Butler 1960, 1961; Gotshall 1978b, c). The few studies of crab populations in estuaries or shallow-water habitats (Butler 1956; Tegelberg and Arthur 1977; Gotshall 1978a; California Department of Fish and Game 1981) have indicated that such areas may be extremely important nursery grounds, but the size and dynamics of estuarine populations have not been statistically determined and, furthermore, the contribution of estuarine habitats to offshore stocks has not been adequately assessed. Orcutt et al. (1978) estimated that 50-80% of crabs caught by the fishery in the Gulf of the Farallones spend some of their life cycle in the San Francisco-San Pablo Bay complex. Benefits derived from estuarine early life history may include enhanced growth rates, more abundant food, and refuge for postlarval and juvenile crabs from larger, older age classes that act as competitors and predators (Botsford and Wickham 1978).

Quantitative studies of *C. magister* in major estuaries are timely and imperative. The demise of the San Francisco fishery prompted a 5-yr investigation of *C. magister* biology in that region (California Department of Fish and Game 1981), and hypotheses for the decline include alterations of estuarine habitat and water quality. In addition, channel dredging practices in west coast estuaries kill hundreds of thousands of crabs annually (Stevens 1981). Armstrong et al. (1982) estimated that a proposed channel modification project in Grays Harbor, Wash., could entrain and kill 2.5 million crabs over a 2-yr period. Knowledge of estuarine crab population dynamics and ecology of juveniles is required to gauge the relative importance of such habitat to the species, and to mitigate impacts of estuarine development on juvenile stages.

MATERIALS AND METHODS

Study site

Grays Harbor is a shallow drowned river basin

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estuary with an extensive littoral zone and a wide variety of substrate types (Fig. 1). Sampling stations were established primarily along the existing navigation channel in accord with a concurrent study to assess the impact of dredging on Dungeness crabs (Armstrong et al. 1982). Habitats represented include deeper sandy channels (stations 1-3), shallow sand (station 4), sand-mud (stations 6 and 7), mud (stations 8-12), and those adjacent to eelgrass (*Zostera marina* and *Z. noltii*) beds (station 5) (Table 1; Fig. 1). Fifteen sublittoral strata were established for the purpose of estimating population abundance, and sampling stations were located approximately at the center of each (Fig. 1). However, strata 14 and 15 contained no regularly sampled stations because these areas were outside the primary focus of our contract. The boundaries of each stratum were defined by the midpoint between sampling stations, or the bottom contours at −5.5 m or 0.0 m (for detailed

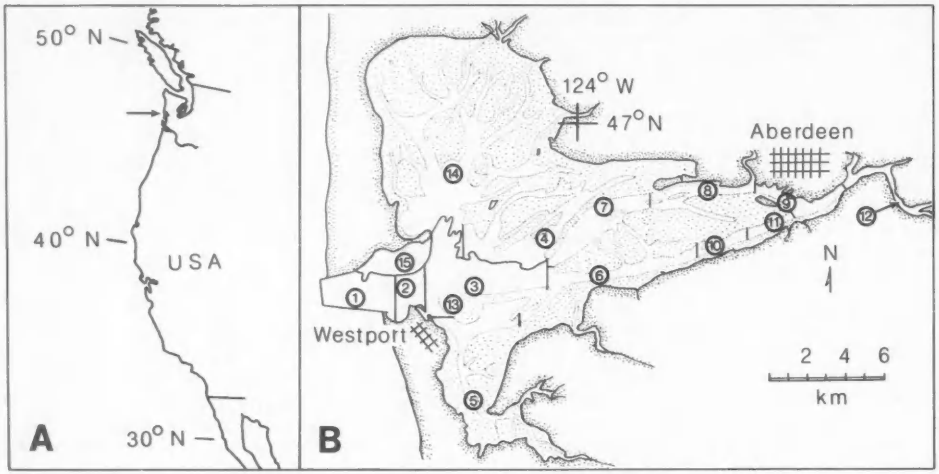

FIGURE 1.—A. West coast of North America. Arrow indicates site of Grays Harbor, Wash.; B. Map of Grays Harbor, showing sites of *Cancer magister* collection (1-13). Stations 14 and 15 represent unsampled strata. Lines separating strata were defined arbitrarily for use in determining crab population size.

TABLE 1.—Location and description of sampling sites for *Cancer magister* in Grays Harbor, Wash.

Station no.	Area (ha)	Gear type[1]	Latitude N	Longitude W	Depth (m)	Bottom type	Comments
1	837	T	46°54'30"	125° 9' 0"	15-18	Sand, cobble	Not sampled in 1981 due to rough water conditions.
2	496	T	46°55'15"	124° 7'20"	13-15	Hard sand	Dredged sediment disposal site.
3	1,507	T	46°55'15"	124° 4'20"	10-15	Sand	Outer harbor channel bottom.
4	1,120	T	46°56'40"	124° 1'10"	3-5	Sand, mud	Shallow outer harbor habitat.
5	658	T	46°51'55"	124° 4'15"	5-8	Sand, mud	Adjacent to extensive eelgrass beds.
6	680	T	46°55'40"	123°59' 5"	6-8	Sand, mud, leafy debris	Near mudflats without eelgrass.
7	656	T	46°57'30"	123°59' 0"	11-14	Mud, sand	Adjacent to eelgrass beds.
8	418	T	46°58'10"	123°55'20"	11-15	Mud	Inner harbor channel bottom.
9	221	T	46°57'40"	123°50'50"	12	Mud	Numerous snags; adjacent to shipping terminals, inner harbor.
10	96	RN	46°56'20"	123°54'15"	3-4	Mud, snags	
11	86	RN	46°57'12"	123°51'15"	3-4	Mud, snags	
12	—	RN	46°57'37"	123°46'18"	3-4	Mud, cobble	Along shore of deep (20 m) river channel.
13		T	46°54'45"	124° 5'15"	0-3	Sand	Intertidal sand flat; no eelgrass.
14	2,653					Mud, sand, eelgrass	Not sampled. Used for population estimate.
15	414					Sand	Not sampled. Used for population estimate.

[1]T = otter trawl; RN = ring net.

descriptions see Stevens 1982). The area of each stratum was determined by planimetry at the level of mean lower low water (NOAA Chart No. 18502 Grays Harbor, 1979 edition).

Sampling Design

Crabs were sampled at stations 1-9 and 13 with a 4.9 m, 4-seam, semiballoon otter trawl net, having 38 mm stretch nylon mesh throughout and a 6 mm cod end liner. Working width of the net was about 3.0 m. Distance towed was measured between buoys placed at the beginning and end points of each trawl, by compass triangulation to stationary objects whose positions were predetermined and located on 7.5-min topographic maps (U.S. Geological Survey). Distances were then converted to area swept and catches expressed as crabs/ha. At stations 10-12, underwater snags prevented trawl operation so crabs were collected by setting collapsible ring nets (76 cm diameter) covered with 12 mm mesh. A "set" consisted of 4 baited nets set 50 m apart and fished for 20 min. Catches were expressed as crabs/net. Trawls and ring net sets were made within 1-2 h of slack low tide in daylight. Occasional plankton tows were made with a 0.5 m diameter conical net of 500 μm mesh, in the spring of 1980 and 1981, to determine if crabs entered the bay as larvae.

Stations 3, 6, 8, and 9 were sampled biweekly from May through October 1980 and at intervals of 4-5 wk thereafter through July 1981. Other stations were generally sampled monthly except when weather or boat problems precluded operations. Most stations were sampled on 13-19 occasions during the 14-mo field study (May 1980 to late June 1981), with the exception of stations 1 and 2 (6 and 10 samples, respectively). Station 13 was sampled quarterly on a diel basis, and complete results from that diel study are reported elsewhere (Stevens and Armstrong 1984). No samples were taken at stations 14 and 15 which were used only to calculate crab populations based on data from adjacent areas (see below).

All crabs were measured to the nearest millimeter across the carapace between the notches just anterior to the 10th anterolateral spines ("carapace width" or cw), sexed, and released. Subsamples were used for width frequencies only in May and June of 1980 and 1981, when early instars were collected in large quantities. Surface and bottom-water samples were collected during each trawl with a modified Van Dorn bottle; temperature was measured to 0.1°C, and salinity determined with a refractometer at room temperature.

Growth Analysis

Cumulative width frequencies of all crabs caught during a given week were plotted on probability paper, and width limits were subsequently defined as the curve inflection points (arbitrarily nonoverlapping) to delimit the size range of each year class through time, according to the method of Cassie (1954). These were compared with frequency graphs for verification. Values were interpolated during weeks in which too few crabs were caught for accurate analysis. Each crab was then assigned to an age-group on the basis of the width limits for each sampling week. Age was defined as the number of years since metamorphosis. Mean widths were calculated for each age group (0+, 1+, 2+, and 3+) and plotted by sampling week. Eighty-seven males (12-132 mm cw) and 74 female crabs (15-115 mm cw) were frozen and returned to the University of Washington where they were opened at the epimeral line and dried to constant weight at 60°C (48-72 h). Only hardshell intermolt crabs were used. Log_{10} dry weight (g) was plotted against $\log_{10}$ carapace width (mm) and regression equations determined for each sex. Mean weights for each age group of crabs were calculated at monthly intervals from mean widths using the regression equation (the 1977 year class was omitted because the regression equation did not represent these larger animals). Weight-specific growth rates (k) per month were calculated by use of the equation

$$W_t = W_0 e^{kt}.$$

The monthly percent weight increase was calculated as $e^k - 1$.

Crab Density Analysis

Because counts of benthic invertebrates usually show a contagious distribution (Elliott 1977), all density data were transformed prior to analysis of variance or regression by

$$X_t = \text{Log}_{10} (\text{density} + 1),$$

where X_t is the transformed variable.

Density was plotted against bottom-water salinity, temperature, and estimated Chehalis River flow by a stepwise multivariate procedure (SPSS REGRESSION) for all trawl and ring net samples.

The effects of season and location on crab density were examined by analysis of variance (SPSS ANOVA procedure). The sampling year was divided into two seasons: spring-summer (March-August) and fall-winter (September-February). The navigation channel was divided into two areas: the outer estuary (stations 2, 3, and 4: station 1 deleted due to lack of winter data points), and the inner estuary (stations 7, 8, and 9). A two-way ANOVA was performed with these two seasons and two station groups as the independent variables, and crabs/ha as the dependent variable.

Population Estimation

Two basic assumptions were made concerning the trawl data: 1) Sampling efficiency of the net was not 100% and varied for each age class of crabs. Efficiency was estimated to be 0.33 for the 0+ age class during summer, and 0.25 in winter, based on comparisons between net catches and visual counts of young instars on mudflats at low tide (see Discussion). Sampling efficiency was estimated to be 0.50 for all other age groups in accordance with Gotshall (1978a). 2) Sampling efficiency was assumed to remain constant and not to vary as a function of changes in crab behavior (e.g., burial or diel activity variations).

Data on crab densities were used from a 12-mo period, June 1980 to May 1981, which was divided into three "seasons": summer (June-August 1980), fall-winter (September 1980-February 1981), and spring (March-May 1981). Population estimates were made for three age groups (0+, 1+, and 2+, the latter including all 3+ animals which were identifiable only in summer 1980) in each of the three defined seasons. A stratified random technique was used, using the following variables (see Cochran 1953):

h	= stratum of harbor
C_{ih}	= catch of crabs in tow i, stratum h
a_{ih}	= area (ha) covered by tow i, stratum h
n_h	= number of tows in stratum h
x_{ih}	= individual estimates of crabs ha^{-1}, from tow i, stratum h
$\bar{x}_h$	= mean catch (crabs ha^{-1}) in stratum h for a given season
A_h	= area of harbor in stratum h (ha)
$s^2_{(\bar{x}_h)}$	= variance of mean $\bar{x}_h$ in stratum h
T	= total number of crabs in harbor.

Data used for population estimates were not transformed as done for ANOVA comparisons because that would have led to complications in the determination of confidence intervals, but only minor changes in the resultant mean densities of crabs. Mean crab density in each stratum was calculated for each age group and season by

$$\bar{x}_h = \frac{\sum_{i=1}^{n} (c_{ih}/a_{ih})}{n_h}.$$

The total number of crabs in each stratum was calculated as $T_h = A_h(\bar{x}_h)$, and the total for the harbor by the sum of all stratum totals,

$$T = \sum_{h=1}^{15} T_h.$$

For strata 1-9, the variance of each stratum total was calculated by

$$V_{(T_h)} = \frac{A_h^2 s^2(\bar{x}_h)}{n},$$

and the variance of the total was calculated by summing the individual variances

$$V_{(T)} = \sum_{h=1}^{9} V_{(T_h)}.$$

Confidence intervals for T were approximated at the 95% level by

$$T \pm t_{(\mathrm{df},\,0.05)} V_{(T)}^{1/2}.$$

Crab abundances in strata which were not sampled by trawl (10, 11, 14, and 15) were calculated using mean density values from nearby strata of similar ecological characteristics. Data were used from strata 6 (for 10 and 11), 5 (for 14), and 3 (for 15). Totals by age group and season for those strata were added to totals for strata 1-9, to obtain totals for the entire estuary. The estuary totals were divided by the estimated trawl efficiency factors to obtain final corrected estimates of crab abundance by age group and season. Confidence intervals for these final estimates could not be computed.

RESULTS

Temperature-Salinity Profile

Grays Harbor has a strong horizontal salinity gradient (Fig. 2). Temperature and salinity were

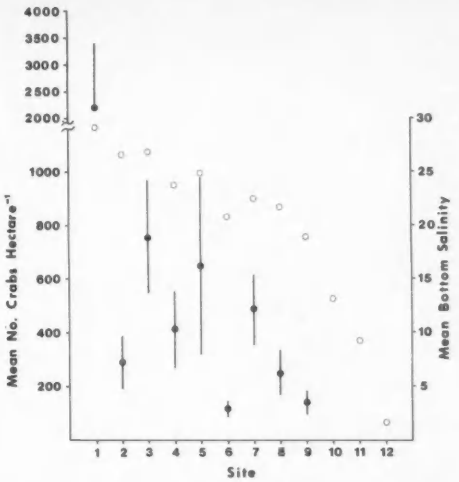

FIGURE 2.—Temperature-salinity profile for crab sampling sites 1-12, Grays Harbor, Wash. Filled circles indicate mean density +1 SE of crabs for the entire study, as determined by trawl; open circles indicate mean bottom salinity at low tide. Crab densities are not plotted for stations 10-12 where ring nets were used.

more stable in the outer estuary, but less so as distance increased eastward from the harbor mouth. At station 3, bottom temperatures ranged from 7°C (winter) to 14°C (summer), while at station 9 they ranged from 5° to 18°C. Vertical stratification was greater toward the head of the estuary and less so in the outer estuary as a result of turbulent mixing. Greatest vertical salinity difference measured during the study was 17‰ at station 9. Grays Harbor receives 70-100 in of rainfall annually, and stratification was greatest during November-March, the period of peak rainfall. Flow rates of the Chehalis River, which contributes 80% of the freshwater inflow, varied from 22.3 m^3s^{-1} in August 1980 to 2,322 m^3s^{-1} in February 1981 (data provided by U.S. Geological Survey).

Spatial Distribution of Crab Population

Complete records (width, sex, age) were obtained for 14,556 crabs. Coefficients of variation averaged 0.53 for the trawls and 0.46 for the ring nets, implying that both techniques had a similar degree of precision.

Mean density of crabs during the 14-mo sampling period was greatest at station 1 (2,190 crabs ha^{-1}), and catches declined with increasing distance from the estuary mouth and decreasing bottom salinity (Figs. 2, 3A). Notable exceptions to this pattern were low densities at stations 6 and 2 (120 and 290 crabs ha^{-1}, respectively; Fig. 3). Station 2 was concurrently being used as a dredged sediment disposal site by the U.S. Army Corps of Engineers.

Crabs caught by ring net were more abundant at station 11, near the eastern (upstream) end of the estuary than at station 10, and averaged 22.9 and 12.7 crabs net^{-1}, respectively, from June to October (Fig. 3F). No crabs were caught at station 12 except in August and September 1980.

Temporal Distribution of Crab Population

Megalops larvae were found as early as 1 April 1980 at station 6, and in densities up to 810/1,000 m^3 at station 5 on 22 April 1980.

Crab densities at all stations were greatest from May to August 1980 (Fig. 3A-E) and declined from September 1980 through January 1981. Lowest densities occurred in October and November 1980, none being >200 crabs ha^{-1} except at station 1. Although monthly variation was great at each station, this general decline in crab density during fall-winter occurred throughout the estuary.

Crab abundance at the three ring-net stations (10, 11, and 12) increased dramatically from June through October 1980, then dropped in November 1980 to a low of <1.0 crabs net^{-1} at all three stations (Fig. 3F). No crabs were caught at station 12 except during August and September 1980, when the salinity reached 9 and 7‰, respectively. Salinity at station 12 was 1.0‰ or less during all other sampling periods.

The *F*-tests showed that mean crab density in the outer estuary (stations 2, 3, and 4) was significantly greater ($P = 0.011$) than in the inner estuary (stations 7, 8, and 9; Table 2). Crab density at all six stations (2, 3, 4, 7, 8, and 9) was significantly greater ($P = 0.001$) in spring-summer than in fall-winter 1980-81. Regression analysis of $\log_{10}$-transformed density data on bottom salinity, temperature, and Chehalis River flow rate showed no significant dependence of trawl catches on these variables, but salinity alone was responsible for about 40% of the variance in crab abundance at the ring net stations (10, 11, and 12; $r^2 = 0.398$, $P = 0.001$).

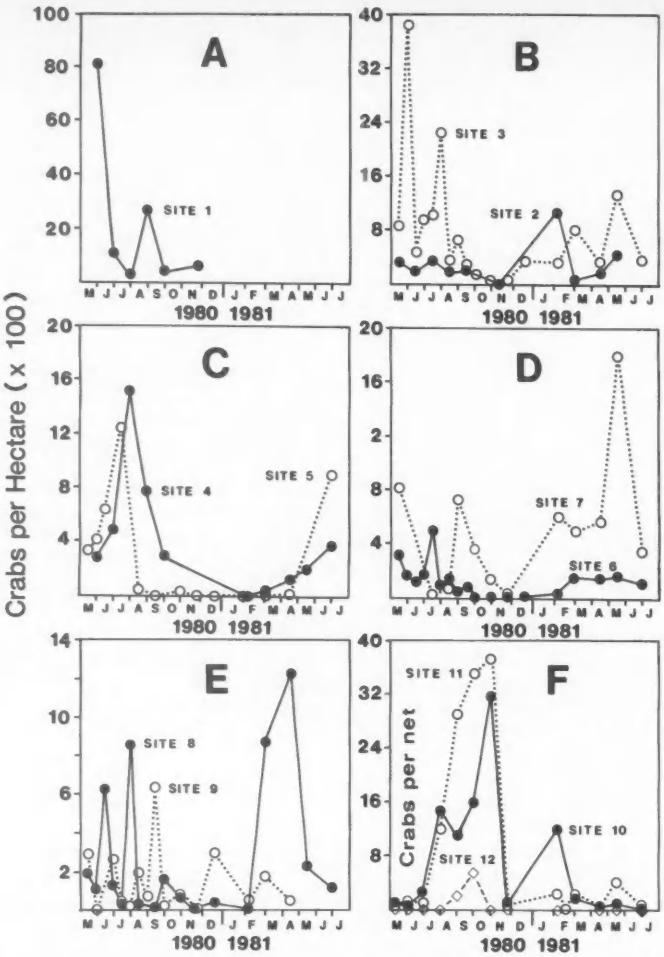

FIGURE 3.—Crab density for all sampling sites in Grays Harbor, Wash., sampled in 1980-81. Trawl sampling sites 1-9 are shown as crabs ha^{-1}; ring-net sampling sites 10-12 are shown as crabs per ring net. Each point represents a single sample.

Age-Structure of Crab Population

Width-frequency distributions for all crabs caught by trawl in the estuary are presented by sampling week in Figure 4. Width limits for each age class were selected so as to be nonoverlapping (Table 3).

The distribution of crabs within the estuary varied with age group. Animals in the 0+ age group were commonly found from station 2-8 at an average of 46 crabs ha^{-1}, and represented 16.6% of total crabs caught in the estuary throughout the entire 14-mo sampling period (Fig. 5). The greatest annual mean density of this age group occurred at station 5 near an area of dense eelgrass. The density of this age group was very low during October-December.

Summer populations of 0+ crabs were about twice as dense at station 5 than at any other (Fig. 6). Visual inspection of mudflats adjacent to this

TABLE 2.—Mean densities of *Cancer magister* in Grays Harbor, Wash., areas and seasons compared by ANOVA. Values are means of original data expressed as crabs ha^{-1}, ± SE, with n in parentheses. F tests were performed on log-transformed data.

Mean densities:	Outer harbor (sites 2-4)	Inner harbor (sites 7-9)	Season means
Spring-summer (March-Aug.)	658 ±146 (29)	358 ±73 (32)	500 ±81 (61)
Autumn-winter (Sept.-Feb.)	229 ±104 (10)	120 ±42 (16)	162 ±47 (26)
Area means	548 ±114 (39)	279 ±53 (48)	

Results of F-tests:

Comparison	df	F-value	Probability level
Seasons	1/83	15.181	0.001
Areas	1/83	6.744	0.011
Interaction	1/83	0.607	0.438

site in May 1982, and at a similar site in stratum 14 in May 1981, revealed that first instar crabs were abundantly distributed on the mudflats at low tide in slight depressions, buried just beneath the sediment surface and in burrows of *Callianassa* spp. Estimated densities were 1-5 crabs m^{-2}, based on random visual observations within an area of the mudflats measuring about 100 m^2. This density was 1-2 orders of magnitude greater than that calculated from trawl catches of this age group. Therefore, it is likely that 0+ crabs were grossly underrepresented in the trawl catch, especially at stations near mudflats such as 4 through 8. The 0+ age group formed <1% of the catch at station 1 and were virtually absent from the ring net stations (10-12).

Crabs in the 1+ age group were by far the most

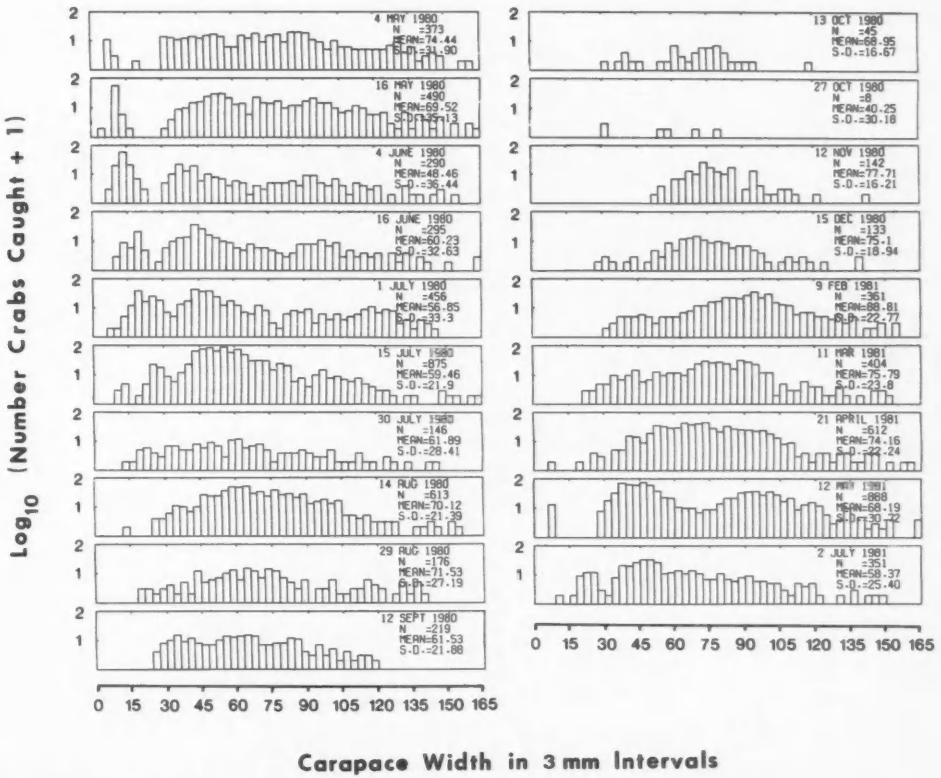

FIGURE 4.—Carapace width frequencies of all crabs caught by trawl at stations 1-9 in Grays Harbor, Wash., 1980-81. Numbers expressed as $\log_{10}$ (catch +1). Box for each sampling period shows date, number of crabs measured, mean carapace width overall (mm), and standard deviation.

TABLE 3.—Upper limit of carapace width range (mm) of *Cancer magister* in Grays Harbor, Wash., for each age/sex group. Selection method was cumulative probability (P) or interpolation (I). The upper limit for age 2+ crabs (lower limit of 3+) was not distinguishable in fall-winter due to low numbers caught. nd = not distinguishable.

	Males				Females			
		Age groups				Age groups		
Date	Method	0+	1+	2+	Method	0+	1+	2+
5/4/80	P	25	60	115	P	30	60	120
5/16/80	I	26	65	120	I	28	69	124
6/4/80	P	27	70	124	P	25	77	127
6/16/80	I	29	70	132	I	27	79	126
6/21/80	P	30	70	136	P	28	80	126
7/1/80	I	32	75	136	I	31	87	127
7/15/80	P	34	85	136	P	37	90	130
7/30/80	I	37	88	134	I	36	91	nd
8/14/80	P	40	92	132	P	36	92	nd
8/29/80	I	43	92	nd	I	41	93	nd
9/12/80	I	45	94	nd	I	45	94	nd
9/26/80	P	46	96	nd	P	50	95	nd
10/13/80	P	46	105	nd	P	50	96	nd
10/27/80	I	46	106	nd	I	52	98	nd
11/12/80	P	46	107	nd	P	54	100	nd
12/15/80	P	46	101	nd	P	52	104	nd
1/17/81	P	44	121	nd	P	55	125	nd
2/9/81	I	44	121	nd	P	54	126	nd
3/11/81	P	45	121	nd	P	61	126	nd
4/4/81	P	47	120	nd	P	56	133	nd
4/21/81	I	15	55	nd	I	15	63	120
5/21/81	P	26	70	127	P	29	75	120
7/1/81	P	29	75	nd	P	29	86	nd

abundant at all stations except 3, averaging 268 crabs ha^{-1} and 54.7% of all crabs over the entire sampling period. Greatest densities occurred at station 1, but these crabs were also abundant at stations 3, 4, 5, and 7 (Fig. 5), i.e., the outer estuary. This group was least abundant at stations 6, 8, and 9, but comprised the largest proportion (73-78%) at the ring net stations (10-12).

The average density of the 2+ age group was 121 crabs ha^{-1} (stations 1-9) equal to 21.3% of all crabs caught. Greatest densities occurred at stations 1 and 3 (Fig. 5). This group was the most abundant at station 3, the only area where the 1+ age group did not predominate.

The 3+ age group was difficult to separate from the 2+ group because the former were caught in low numbers. Of all samples taken during the study, they represented 3% with an average density of 17 crabs ha^{-1}. This group occurred primarily at stations 1-3, with greatest densities at station 1 (Fig. 5).

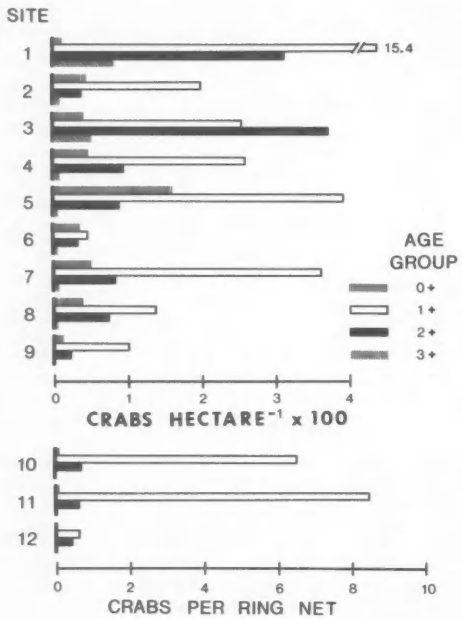

FIGURE 5.—Mean number of crabs per hectare (sites 1-9) and crabs per ring net (sites 10-12) in Grays Harbor, Wash., over the entire study period, by age group.

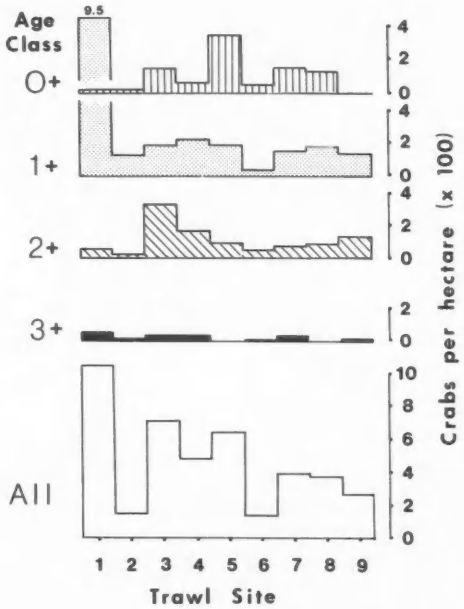

FIGURE 6.—Actual density of crabs caught by trawl at sites 1-9 in Grays Harbor, Wash., June 1980, by age class. Sites 2, 5, and 7 sampled on 4 June; sites 1, 4, and 9 sampled on 16 June; sites 3, 6, and 8 sampled on both dates and averaged. Note greatest abundance of 0+ age group at site 5.

Growth: Width

Crabs in the 0+ age group (1980 year class) increased in width by a factor of 4, from 10 mm in May to 40 mm in October 1980, but growth slowed from then to the following April 1981 when they were about 50 mm wide (Fig. 7). The same pattern of rapid growth during spring and summer was evident among the 1+ and 2+ age groups (1979 and 1978 year classes, respectively), although measurable increases in carapace width were recorded into winter 1981 for these older crabs. Crabs of the 1979 year class grew from 45 to 73 mm between May and October 1980 (factor of 1.6), while the 1978 year-class crabs grew from 84 to 118 mm during the same period, an increase of 1.4. Females had slightly greater mean widths than males up to about 125 mm cw, but the differences were minor (Table 3).

Growth: Weight

Regression equations for $\log_{10}$ dry weight (g) on $\log_{10}$ carapace width (mm) were derived separately for male and female crabs, but were not significantly different. Therefore, a pooled regression equation was calculated for both sexes combined:

$$\text{Log}_{10}\ \text{Weight (g)} = -4.064 + 2.832\ (\text{Log}_{10}\ \text{Width, mm})$$

or

$$\text{Weight (g)} = (8.63 \times 10^{-5})\ \text{Width}^{2.832}$$

($r^2 = 0.985$, $P = 0.0001$; Fig. 8).

Differences in width/weight and width/age relationships between male and female crabs would probably increase at sexual maturity, which occurs about 2 yr after metamorphosis, and at widths of 93-122 mm for males and 100-105 mm for females (Butler 1960, 1961; Poole 1967). Growth data presented herein are probably valid only for male crabs <132 mm and female crabs <115 mm width.

Changes in mean weight with time (Fig. 9) probably represent a continuous curve, but there appeared to be an inflection point in late August that separated spring-summer and fall-winter growth stanzas. Therefore, k values were calculated for the periods May-August and September-April.

Monthly weight-specific growth rates were greater in spring-summer than in fall-winter for all age groups but decreased with size (Fig. 9). Specific growth rates were greatest for 0+ age group crabs in their first summer during which the average monthly weight increase was 206% (Table 4). Growth decreased to an average 15.8% per month during the winter. Growth rates increased again for age 1+ crabs in their second summer (31% per month), but were lower than experienced in their first year. This pattern was found for all age groups. Crabs in the 2+ age group (probably at sexual maturity) increased in weight 25% per month in the summer of 1980, but only 6.5% per month during the following winter (Table 4). First

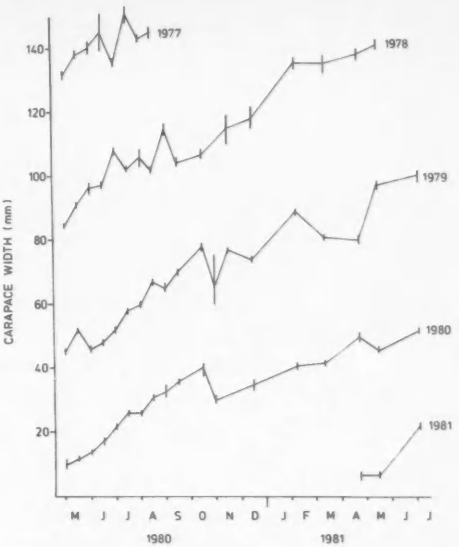

FIGURE 7.—Mean width of four age groups of crabs (0+, 1+, 2+, 3+) in Grays Harbor, Wash., 1980-81. Mean width (+1 SE) shown for each sampling period was determined by graphical analysis of width-frequency data or interpolation (see Table 3).

TABLE 4.—Weight-specific growth rates (k) and percent weight increase of three year classes of *Cancer magister* in Grays Harbor, Wash. Weight calculated from mean carapace widths of each year class by regression equation (see Figure 8). Growth per month calculated for spring-summer (May-August) and fall-winter (September-April) growth stanzas (see also Figure 9).

	Dry weight (g)			Mean growth per month			
				Spring-Summer		Fall-Winter	
Year class	4 May 1980	29 Aug. 1980	22 Apr. 1981	k	% weight increase	k	% weight increase
1980	0.02	1.75	5.56	1.118	206	0.147	15.8
1979	4.02	11.75	21.46	0.268	31	0.075	7.8
1978	24.30	59.70	98.71	0.225	25	0.063	6.5

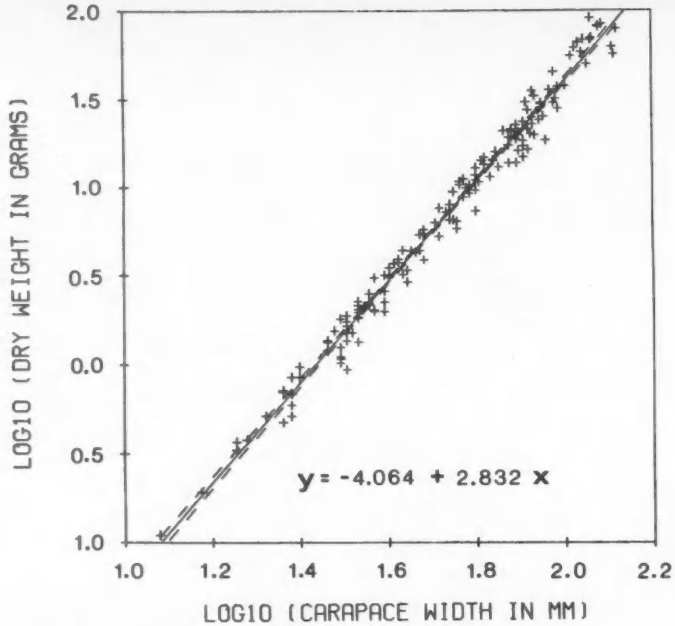

FIGURE 8.—Regression of $\log_{10}$ dry weight (g) on $\log_{10}$ carapace width (mm) for 87 male (12-132 mm) and 74 female (15-115 mm) *Cancer magister* from Grays Harbor, Wash. Observations (+), regression line (solid), and 95% confidence interval about the regression line (dashed) are shown.

instar crabs (7 mm cw) of 0.02 g dry weight increased in dry biomass 282 times by the time they reached the 6th or 7th instar (about 50 mm cw), weighing 5.7 g the following April (Fig. 9). Some may have reached 70 mm by that time, weighing 14.7 g, an increase of over 700-fold. Second-year crabs increased in dry biomass 5.3 times, from 4.0 to 21.5 g. Third-year crabs increased from 24 to 99 g, a dry biomass increase of 4.1 times.

DISCUSSION

Recruitment and Distribution in the Estuary

Megalops larvae probably metamorphosed to the first postlarval stage in Grays Harbor, since trawl collections included second instars on 4 May 1980 and first instars in April and May 1981. Cast exuviae of these stages were abundant on beaches of the outer estuary in early May 1982. Larval densities in the estuary were at the low end of the range of densities found by Lough (1976) off the Oregon coast in 1970-71 (100-8,000/1,000 m^3). In contrast, no megalops larvae were found in San Francisco-San Pablo Bays during 4 yr of surveys by the California Department of Fish and Game, which concluded that crabs entered that estuarine system only after metamorphosis (Orcutt et al. 1975, 1976).

Once inside Grays Harbor, *C. magister* showed an ontogenetic change in habitat selection, i.e., centers of abundance changed with age. Eelgrass beds may be the preferred habitat of the first postlarval stages, because catches of 0+ crabs were most abundant near those areas (Figs. 5, 6). Butler (1956) also found that the most abundant concentrations of early instars along the northern shore of Graham Island, Canada, were associated with the presence of *Zostera marina* in sheltered inlets. However, this age class was widely distributed from stations 1 to 9.

Crabs in the 1+ age group (size range 50-90 mm cw) were the most abundant. Although their dis-

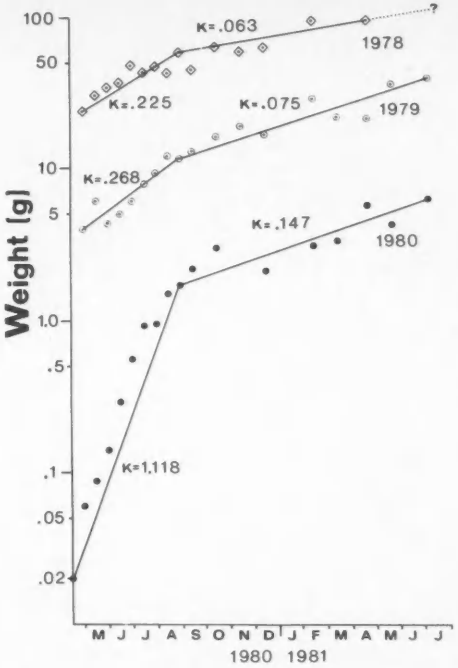

FIGURE 9.—Growth rates of *Cancer magister* from Grays Harbor, Wash. Points represent $\log_{10}$ mean dry weight calculated from mean width by regression equation. Straight lines (fitted visually) show slope of growth curve (k) for summer and winter growth stanzas of 1980 (0+), 1979 (1+), and 1978 (2+) year classes. Growth stanzas arbitrarily separated at 28 August 1980.

tribution greatly overlapped that of the 0+ age class, age 1+ crabs showed proportionally less use of low-salinity stations such as 6, 8, and 9. Although this group was also abundant near eelgrass beds, they were restricted to the subtidal channels and showed only intermittent use of mudflat areas during high tides, whereas many crabs of the 0+ group remained in the littoral zone at low tide.

The 2+ age group, consisting of sexually mature crabs (Poole 1967), was abundant only at the outer estuary stations (1, 3, 4, 6, and 7). Many crabs probably migrate out of the harbor before reaching age 3+. This hypothesis is supported by the scarcity of age 3+ crabs east of station 3 and the total absence of gravid females from trawls taken in the estuary, although many trawls were made during the spawning season (October-March). Apparently, most mature females leave the harbor to spawn. Stressful salinity and temperature, high larval predation in the estuary, or inadequate larval food supplies might have created selection pressures for spawning females to seek water offshore with the proper environmental conditions for higher egg and larval survival.

Crab Population Estimates

A more important question than that of local crab densities at several stations is that of total population abundance throughout the estuary, determined for different seasons and age classes. Such a calculation is of interest in order to gauge 1) the potential use of the estuary by the species and the 0+ age class in particular; 2) the theoretical contribution made by the estuarine population to the commercial fishery; and 3) the potential impacts of estuarine development (e.g., dredging and landfill) on resident populations. The former two points are addressed in this discussion.

Trawl Efficiency Estimates

In order to extrapolate crab density values at each station to abundance within the corresponding stratum, some measure of trawl efficiency was needed. Examinations of mudflat areas (stations 5 and 14) in May of 1981 and 1982 showed very high densities of 0+ age crabs, ranging from 1 to 5 crabs m^{-2}. This estimate was conservatively reduced to 1 crab m^{-2}, and we assumed that only 50% of the available estuarine bottom (Fig. 1B) was utilized by early instars (excluding the inner estuary and perimeter which had lower salinities and had produced few or no crabs of this age group). This "corrected" density of 0.5 crabs m^{-2} (5,000 crabs ha^{-1}) was about 30 times the mean summer density of age 0+ crabs at station 5 (162 crabs ha^{-1}) as estimated by trawl; thus trawl efficiency in that season was about 0.033 (more recent studies have shown early instar densities to equal or exceed 10 m^{-2} in 1983; D. Armstrong, unpubl. data). In winter and spring, 0+ age group crabs were large enough to be sampled more effectively, but probably not as effectively as larger crabs; thus a factor of 0.25 was used in both of those seasons. An efficiency factor of 0.5 was applied to all other age groups, in accordance with Gotshall (1978a).

Abundance Calculation

For the nine strata of Grays Harbor sampled by

trawl, the total number of trawl-catchable crabs present in 1980-81, ±95% confidence intervals, were summer, 4.3 ± 1.7 million crabs; winter, 1.3 ± 0.7 million crabs; and spring, 2.6 ± 1.2 million crabs (Table 5). However, stratum 1 (837 ha) was excluded from the spring estimate due to lack of data, but was reincluded later, using density estimates from adjacent stratum 3. Totals for the other nonsampled strata (10, 11, 14, and 15) were added to totals for the trawl-sampled strata, and the sums for each age group were divided by the trawl efficiency estimates described above. Final calculated numbers for the total crab population were summer, 39.0 million crabs; fall-winter, 3.3 million crabs; spring, 7.8 million crabs (Table 5).

The 1980 year class, which was extremely abundant in the summer of 1980, virtually disappeared during the following winter, and reappeared in spring of 1981. Some hypotheses for this decline and recovery include winter hibernation, migration to nonsampled areas (e.g., stratum 14), and temporary egress from the estuary. Natural mortality probably contributed substantially to the decline as well.

Due to the speculative nature of these estimates and the underlying assumptions concerning trawl efficiency and proportion of habitat utilized, it was not possible to compute confidence limits on these final estimates. The estimates of total population abundance in the estuary suggest a tremendous increase in summer with the influx of 0+ crabs as megalopae and first instars, and an increase in 1+ animals as well. This estimate of 39 million crabs is the highest estuarine crab population abundance yet reported. The only other reported estimate, that of 9.3 million crabs in the San Francisco-San Pablo estuary complex during 1975 (Orcutt 1978), is based on a much less systematic survey than ours and does not correct for poor gear efficiency in regards to the small size of early instars. Furthermore, this latter estuarine system represents an area (500 km²) five times that of Grays Harbor.

The accuracy of our estimates of population abundance can be qualitatively assessed by comparison of trawl density data with that of other studies (Gotshall 1978a; Orcutt et al. 1975, 1976; Orcutt 1977, 1978; Table 6). Generally, there is great seasonal variation, but densities estimated in Grays Harbor are in accord with values for Humboldt Bay and San Francisco Bay. Extrapolations to total abundance indicate that large populations of juvenile crabs may use other coastal estuaries as well. Even relatively small estuaries in Oregon, such as Tillamook, Netarts, Yaquina, and Coos Bay, could support large populations of 0+ crabs, considering their small biomass (0.2 g dry weight). The principal benefits of these estuaries are probably refuge from larger cannibalistic conspecifics (Botsford and Wickham 1978; Stevens et al. 1982), more abundant food, and possibly accelerated growth as a result of food supplies and warmer temperatures than offshore waters.

TABLE 5.—Estimation of *Cancer magister* population in Grays Harbor, Wash., for 1980-81. All values are numbers of crabs except efficiency factors and percentages. C.I. = confidence interval.

Season/ Age Class[1]	Strata sampled by trawl (sites 1-9) n (×10³)	Variance of n (×10⁶)	df	C.I.[2] (×10³)	Strata not sampled[3] (n ×10³)	Sum of crabs (×10³)	Efficiency factor	Total crabs (×10³)	% of total
Summer									
0+	485	9	36	188	470	955	0.033	28,942	74.2
1+	2,979	555	36	1,511	982	3,961	0.5	7,922	20.3
2+	851	19	36	279	228	1,079	0.5	2,160	5.5
Total	4,315	687	36	1,681	1,680			39,024	100.0
Winter									
0+	182	14	28	244	6	188	0.25	753	23.0
1+	1,070	82	28	588	87	1,157	0.5	2,311	70.7
2+	97	10	28	65	7	104	0.5	207	6.3
Total	1,349	123	28	720	100			3,271	100.0
Spring									
0+	146	8	13	189	87	233	0.25	931	11.9
1+	1,176	151	13	918	307	1,483	0.5	2,965	38.0
2+	1,246	342	13	1,262	707	1,953	0.5	3,904	50.1
Total	2,568	290	13	1,163	1,101			7,800	100.0

[1]See Table 3 and Figure 7 for size of these age classes throughout the year 1980-81.
[2]Values for $t_{(0.05)}$: summer = 2.029, winter = 2.048, spring = 2.160.
[3]See text for explanation of estimates based on data of adjacent trawl stations.

TABLE 6.—Comparison of *Cancer magister* densities in Grays Harbor, Wash. (this report); Humboldt Bay, Calif. (Gotshall 1978a); and San Francisco-San Pablo Bay, Calif. (Orcutt et al. 1975, 1976; Orcutt 1977). Data are not corrected for gear efficiency.

Bay	Season	Year	Transect		No. crabs/ha
			Method	Area (m^2)	
San Francisco-	Summer	1975-77	Trawl	[1]1,500	90-340
San Pablo, Calif.	September	1977-78	Trawl	1,500	13-170
Humboldt Bay, Calif.	January	1967	Trawl	2,400	4,910
	August	1967	Trawl	2,400	300
	April	1968	Trawl	2,400	140
	August	1968	Trawl	2,400	1,280
	October	1968	Trawl	2,400	930
		(Mean of trawl samples, 1967-68 = 890)			
	August	1967	Scuba	140	520
	April	1968	Scuba	140	0
	August	1968	Scuba	140	4,480
	October	1968	Scuba	140	280
		(Mean of scuba samples, 1967-68 = 1,080)			
Pacific Ocean, near	October	1968	Trawl	[2]6,667	0-9,400
Humboldt Bay, Calif.	November	1968	Trawl	6,667	0-36,000 ($\bar{x}$ = 800)
Grays Harbor, Wash.	June	1980	Trawl	variable	200-1,000
Outer Harbor	December	1980	Trawl	1,400	310
	May	1981	Trawl	2,000	1,320

[1]Distance estimated as 50 m/min.
[2]Area estimated as distance (given) × ⅗ (headrope length).

Growth

Dry weight increased 282 times between first instar (0.2 g) and sixth instar (5.7 g) during the first year. Other authors have not presented growth data as changes in weight, but rather as increases in carapace width. Crabs in Grays Harbor grew from about 7 mm to 50+ mm cw during 1980-81, which is similar to values reported by Cleaver (1949) and Butler (1961). However, Poole (1967) concluded that crabs in Bodega Bay, Calif., reached 75 mm (range 50-100 mm) by 1 yr after metamorphosis. This would represent fairly rapid growth, but close to the upper limits of crab growth rates in Grays Harbor.

In contrast to Grays Harbor, Tasto (1983) stated that juvenile crabs spend only 1 yr in San Pablo Bay, and reach 100 mm by the end of that time (twice the growth rate of ocean crabs and Grays Harbor crabs). He concluded that the estuarine population was a single year class and was almost completely replaced by a new year class each spring, a situation very different from Grays Harbor where at least three year classes are present constantly. The San Francisco data may have been misinterpreted, perhaps caused by use of collecting gear (mostly ring nets) that selected larger crabs and resulted in a frequency mode near 100 mm cw that may have actually represented older 1+ age group crabs.

Unfortunately, growth data are not available for 0+ age Dungeness crabs that metamorphose directly offshore for comparison with estuarine populations. Presumably, colder bottom-water temperatures offshore (8°-10°C) would cause metabolic, growth, and general energetic depression of these animals relative to rates in warmer (14°-18°C) estuaries. Studies of offshore juvenile populations are much needed in this regard.

Importance of Grays Harbor to Commercial Fisheries.

The potential contribution of Grays Harbor to the commercial landings of *Cancer magister* was calculated by assigning various mortality rates to the 1980 year class for a period of 3.5 yr, i.e., until recruitment to the fishery. Jow (1965) estimated annual natural mortality of adult male crabs to be 15% per year (M = 0.165, exponential). Mortality rates for juveniles are unknown, so we have assumed a range of 0.5-0.8. From an initial population (N_0) of 28.9 million juvenile crabs in summer of 1980, the number surviving 3.5 yr (N) was calculated from the equation

$$N = N_0 e^{-zt}$$

where z represents the annual mortality rate and t is the time interval. Values of z used were 0.8 for the first half year (t = 0.5), 0.5 for the second half year, and 0.2 (as above) for the remaining 2.5 yr necessary to reach legal size, assuming crabs enter the fishable population at that age, as suggested by Cleaver (1949). At these mortality rates, about 9.2 million adult crabs might remain by

December 1983, of which about half, 4.6 million, would be males subject to the commercial fishery. If an equivalent number of crabs were available from the 1980 recruitment to Willapa Bay, a large bay equaling or exceeding Grays Harbor in area and located about 20 km south, then about 9.2 million legal male crabs of estuarine origin might be available to the commercial fishery in 1984-85 from larvae and early instars that utilized these two Washington estuaries in 1980-81.

Washington coastal crab landings for the period 1971-80 have averaged 3,500 t/yr (PMFC 1981), or about 3.85 million crabs (at 0.9 kg/crab). Thus, these two bays could theoretically serve as nursery grounds for more than enough crabs necessary to maintain a viable commercial fishery in Washington. However, landings over the past 40 yr have fluctuated from 1,000 to 8,000 t, with a 9-12 yr period, so it is impossible to predict how the estimated contribution of the 1980 year class will compare to 1984 commercial landings.

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AGE, GROWTH, AND MORTALITY OF GRAY TRIGGERFISH, *BALISTES CAPRISCUS*, FROM THE NORTHEASTERN GULF OF MEXICO

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ABSTRACT

Age, growth, and mortality of gray triggerfish, *Balistes capriscus*, from the northeastern Gulf of Mexico were estimated from sections of the first dorsal spine of 1,746 fish. The oldest female was estimated to be 12 years old and the oldest male was 13 years old. The von Bertalanffy growth equations, using weighted means, were as follows: males, $l_t = 491.9\ (1 - e^{-0.382(t-0.227)})$ and females, $l_t = 437.5\ (1 - e^{-0.383(t-0.150)})$, where l = fork length in millimeters and t = age in years. The mean annual mortality rate as determined by four methods of analyses (based on number of fish at age) ranged from 0.32 to 0.53. The weight-length relationships of gray triggerfish were males, $W = 6.71505 \times 10^{-6}\ L^{3.187}$, and females, $W = 1.3939 \times 10^{-5}\ L^{3.065}$, where W = weight in grams and L = fork length in millimeters.

Exploitation of fish from the northeastern Gulf of Mexico by recreational and commercial fishermen has created a demand for underutilized fish resources. One of the abundant fish resources that is being subjected to exploitation is the gray triggerfish, *Balistes capriscus*. A dramatic increase in demand for this species can be seen in the commercial landings on the west coast of Florida: 7.8 t in 1967 and 26.7 t in 1977 (Anonymous 1967, 1977).

This species is known to occur in the western and eastern Atlantic. In the western Atlantic, its range is from Nova Scotia to Argentina, including the Gulf of Mexico (Briggs 1958; Moore 1967). In the Gulf of Mexico, the gray triggerfish is a primary reef fish inhabiting the area between 12 and 42 m in depth (Smith 1976), except for its first year of life when it is planktonic and associated with *Sargassum* (Dooley 1972).

The harvest of the gray triggerfish in the northeastern Gulf of Mexico and its utilization of reef habitats has created a need to know more about the biology of this species, especially age, growth, and mortality. Age and growth of gray triggerfish, using the first dorsal spine, has been reported only for the southwestern coast of Africa (Anonymous 1980; Caveriviere et al. 1981). This paper reports the results of our investigation on age, growth, and mortality, using the first dorsal spine of gray triggerfish from the northeastern Gulf of Mexico.

METHODS AND MATERIALS

The hook and line fishery for gray triggerfish off Panama City, Fla., was sampled from May 1979 to March 1982. During this period, 2,808 fish were sampled and from each the fork length in millimeters and total weight in grams measured and recorded. The sexes of the fish were also recorded when determinable by gross examination of the gonads. First dorsal spines were available from 1,746 of the 2,808 fish in the collection. Total length (TL), standard length (SL), and fork length (FL) were measured in millimeters from 100 fish to develop length conversion formulas.

The first dorsal spines were processed for examination as follows: 1) removing the first 5 mm of spine shaft above the condyle with a Dremel[2] tool; 2) placing the shaft section on a mounting tag using Lakeside No. 70c thermoplastic cement and sectioning the shaft using the method described by Berry et al. (1977); 3) removing three 0.18 mm thick serial sections from the cement with 50% isopropanol; and 4) mounting the clean sections in 20% Piccolyte cement (20% Piccolyte, 80% xylenes) on glass slides.

Spine cross sections were examined and measured using a closed-circuit television using a 50

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[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

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mm 3.5 macro lens which projected an image of the section on to a monitor screen at 20× magnification. Illumination was by transmitted light. Translucent (light) bands on the cross sections were counted and the distances (in millimeters) from the center of the spine to the distal edge of each band was measured. The spine radius (R) was defined as the maximum distance (in millimeters) from the center of the section (appears as a small hole) to the posterior distal edge (Fig. 1).

Additionally, before the spines were sectioned, the anterior-posterior thickness (T) of 200 dorsal spines was measured to the nearest 0.01 mm at the sectioning site.

The type of growth (opaque = dark, translucent = light) of the margin of each section was noted. The sections were read three times.

The relationships of R, T, and body weight to FL and the relationships between TL, SL, and FL were determined by least squares methods following the suggestions of Ricker (1975). A computer program by Abramson (1971) was used to fit weighted back-calculated mean length at age to von Bertalanffy growth curves. The growth equation (von Bertalanffy 1938, 1957) and values were as follows:

$$l_t = l\,(1 - e^{-K(t-t_0)})$$

where l_t = length at age t,
l = asymptotic length,
K = growth coefficient,
t_0 = time when length would theoretically be zero.

Estimates of annual mortality (a), annual survival (s), and instantaneous mortality (i) were developed for the total collection (2,808 fish) (Ricker 1975). Length-frequency data were converted to age-frequency distribution (N_y = number of fish caught in age class y) by applying age-length keys. Ages III through IX of the resultant catch curves were analyzed by the methods of Heincke (1913), Jackson (1939), Robson and Chapman (1961) and by finding the slope (m) of a regression line fitted to $l_n(N_y)$ and y and substituting the equation $a = 1 - e^m$.

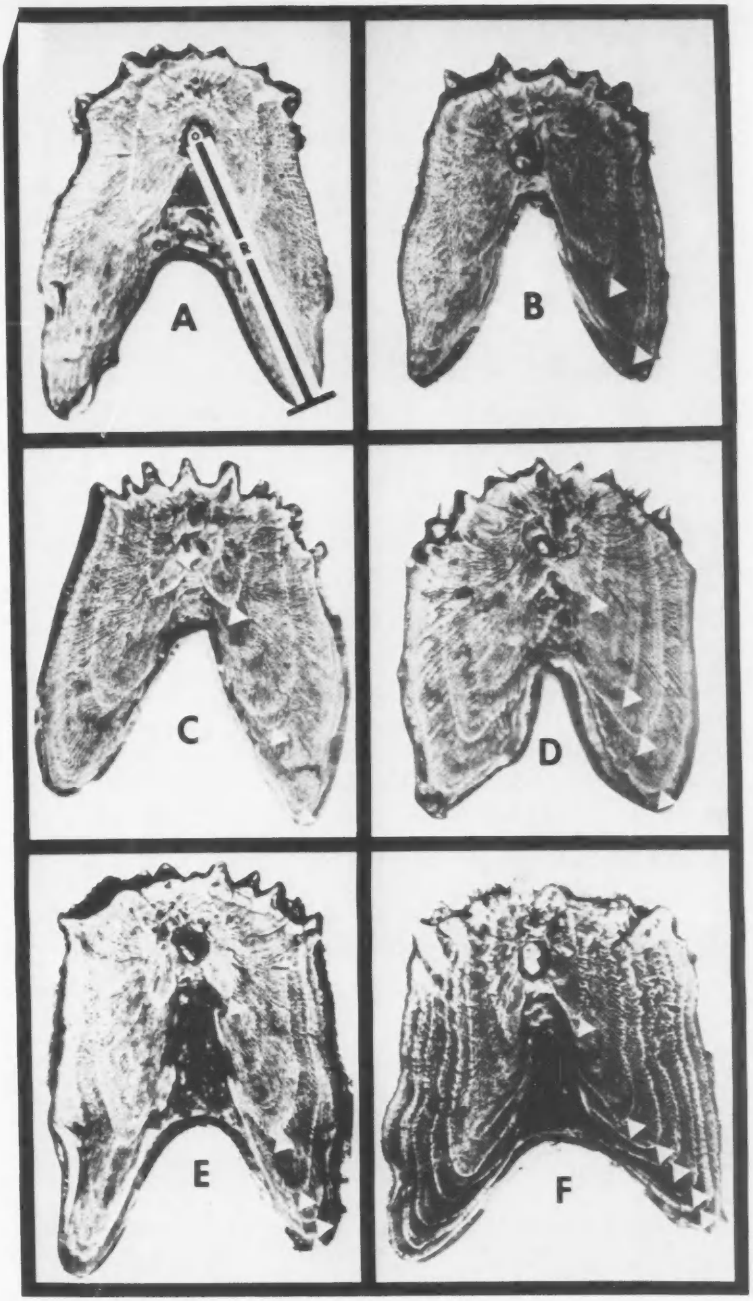
FIGURE 1.—Sections of gray triggerfish first dorsal spines from fish collected off Panama City, Fla. (A) Spine section from a 1-yr-old male (263 mm FL) collected 4 September 1980 with spine radius R labeled. (B) Spine section from a 2-yr-old female (336 mm FL) collected 11 September 1980. (C) A 3-yr-old female (315 mm FL) collected 8 August 1980. (D) A 4-yr-old male (350 mm FL) collected 13 August 1980. (E) A 5-yr-old female (331 mm FL) collected 24 September 1980. (F) A 6-yr-old male (477 mm FL) (seventh mark forming on margin) collected 25 June 1980.

RESULTS

A positive relationship was found between the growth of the first dorsal spine and FL. The relation between FL and R was as follows: FL = $4.58\ R^{0.951}$ with a correlation coefficient (r) of 0.84. The relation between FL and T was as follows: FL = $24.87\ T^{1.422}$ with r = 0.89. The variation in the two relationships probably resulted from the slight tapering of the spine in the area from which the sections were taken and the effect of sectioning. The FL-R relationship was used for back-calculation of sizes at previous ages. The spine sections possessed distinct dark-light banding patterns (Fig. 1) and the agreement between readings as to the numbers of bands was 98% [Beamish and Fournier's (1981) index of average error was 0.0072]. The translucent (light) band formation occurred during spring and summer (April to October with a peak during June-July), and the mean marginal opaque increment was least during this period of time (Table 1). We thus considered the translucent bands on the first dorsal spines to be annular

TABLE 1.—Percent frequency of dorsal spines with translucent (light) margins and mean marginal measurements of opaque (dark) margins in millimeters for gray triggerfish from northeast Gulf of Mexico, 1979-82.

	Month											
	1	2	3	4	5	6	7	8	9	10	11	12
Percent of fish with translucent margins	0.00	0.00	0.00	52.27	41.86	56.70	53.59	23.79	2.40	0.90	0.00	0.00
Mean opaque marginal increment for fish												
2 light bands	—	—	1.40	1.24	1.09	0.74	0.82	0.64	1.00	1.70	—	—
3 light bands	—	0.79	0.49	0.59	0.60	0.58	0.56	0.36	0.50	—	—	—
4 light bands	—	0.56	0.47	0.43	0.52	0.48	0.56	0.38	0.60	—	—	—
5 light bands	—	0.44	0.24	0.26	0.06	0.24	0.37	0.037	—	—	—	—
Total number of fish	6	19	83	88	215	194	209	248	250	111	97	13


A
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F

deposits and suitable for age determination. Lengths varied within age classes and length ranges overlapped between age classes (Tables 2, 3, 4). For example, males with three annuli (translucent bands) ranged from 258 to 537 mm FL and those with four annuli ranged from 250 to 549 mm FL. There was, however, a general trend of increasing modal length with increase in age.

The gray triggerfish is a moderately long-lived species. The oldest male was estimated to be 13 yr old (544 mm FL) and the oldest female was 12 yr old (561 mm FL).

The back-calculated and empirical sizes at age are presented in Tables 5, 6, and 7. The average mean back-calculated length at age for males was slightly (5-50 mm FL) larger than that for females at age 1-9, after which the females were larger. Only three fish were collected that were older than 9 yr; thus the reversal of the trend is probably an artifact caused by few samples.

The von Bertalanffy growth parameters varied slightly between males, females, and all fish. The von Bertalanffy equations were:

$$\text{males } l_t = 491.9(1 - e^{-0.382(t-0.227)}),$$

$$\text{females } l_t = 437.5(1 - e^{-0.383(t-0.150)}),$$

$$\text{all fish } l_t = 466.0(1 - e^{-0.382(t-0.189)}).$$

TABLE 2.—Length composition, in percent, of male gray triggerfish by age groups from northeast Gulf of Mexico, 1979-82.

Length group (FL mm)	Age in years										Total number of fish
	0	1	2	3	4	5	6	7	8	9	
150-199	50.00	50.00									2
200-249		50.00	50.00								18
250-299		14.46	44.58	36.14	3.62	1.20					135
300-349		0.66	26.32	42.10	25.66	2.63	1.97	0.66			307
350-399			9.26	35.80	32.72	18.52	3.70				339
400-449			1.48	18.52	29.62	25.19	15.56	5.93	3.70		233
450-499			11.02	12.24	26.53	29.59	16.34	9.18	4.08	1.02	155
500-549				3.30	27.47	30.77	27.47	8.79	1.10		121
550 and larger						66.67	8.33	16.67		8.33	24
Total	1	23	184	371	339	229	117	47	19	4	1,334

TABLE 3.—Length composition, in percent, of female gray triggerfish by age groups from northeast Gulf of Mexico, 1979-82.

Length group (FL mm)	Age in years												Total number of fish
	1	2	3	4	5	6	7	8	9	10	11	12	
200-249	41.67	33.33	25.00										19
250-299	5.04	42.86	33.61	15.97	0.84	1.68							207
300-349	0.47	14.08	44.61	26.29	7.98	4.69	1.41	0.47					453
350-399		4.64	23.84	35.76	23.18	10.60	1.98						304
400-449			15.38	27.69	21.54	18.46	9.23	3.08	4.62				122
450-499		2.63	7.89	21.06	28.95	26.32	7.89		5.26				74
500-549			4.55	22.73	22.73	18.18	9.09	9.09	13.63				40
550 and larger				20.00	40.00	20.00						20.00	9
Total	20	175	374	321	168	107	35	10	17	0	0	1	1,228

TABLE 4.—Length composition, in percent, of gray triggerfish (all fish) by age groups from northeast Gulf of Mexico, 1979-82.

Length group (FL mm)	Age in years													Total number of fish
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	
150-199	50.00	50.00													2
200-249		47.83	39.13	13.04											32
250-299		9.13	42.47	35.16	11.42	0.91	0.91								365
300-349		0.47	18.27	41.69	26.93	7.72	3.75	0.94	0.23						848
350-399			7.12	31.05	34.47	19.09	6.84	1.43							691
400-449			0.90	16.59	28.70	25.11	16.59	7.17	3.14	1.38	0.45				418
450-499			1.36	10.20	26.53	28.57	19.73	8.84	2.73	2.04					244
500-549				4.23	27.37	28.20	24.79	8.36	2.58	4.37				0.10	172
550 and larger					5.00	50.00	15.00	10.00	5.00	10.00			5.00		36
Total	1	53	373	805	737	445	249	92	29	22	1	0	1	1	2,808

The weight-length relationships for gray triggerfish computed for the equation $W = aL^b$, where W is weight in grams and L is FL in millimeters, were as follows:

males $W = 6.7105 \times 10^{-6}\ L^{3.187}$, $r = 0.97$, $n = 169$,

females $W = 1.393 \times 10^{-5}\ L^{3.065}$, $r = 0.93$, $n = 167$,

TABLE 5.—Back-calculated fork lengths (mm) at age for male gray triggerfish from the northeastern Gulf of Mexico, 1979-82.

Age group	Mean length ± 1SD at capture	N	Average back-calculated FL at age												
			1	2	3	4	5	6	7	8	9	10	11	12	13
I	250.0 ± 29.0	18	137.7												
II	313.4 ± 41.8	99	123.9	248.0											
III	357.4 ± 55.8	192	119.2	243.0	319.6										
IV	407.8 ± 66.6	186	124.1	244.2	322.8	376.3									
V	450.6 ± 56.2	134	128.2	245.1	324.7	381.8	427.0								
VI	461.9 ± 56.0	72	132.2	245.3	309.7	364.3	409.8	443.2							
VII	474.5 ± 51.5	28	126.3	231.8	301.2	350.7	390.7	430.5	458.7						
VIII	462.5 ± 27.4	10	134.0	236.5	307.4	344.3	372.8	399.5	429.7	448.6					
IX	511.5 ± 78.5	2	165.8	293.1	323.0	362.0	389.8	424.7	468.7	489.9	504.0				
XIII	544.0 ± —	1	91.0	308.5	395.0	452.7	461.5	479.0	492.1	496.5	500.8	509.5	513.8	526.8	535.4
Weighted mean			124.9	244.3	319.6	373.7	415.5	436.2	452.9	458.7	502.9	509.5	513.8	526.8	535.4
± 1SD			± 41.0	± 49.4	± 55.5	± 60.9	± 60.1	± 56.8	± 48.6	± 32.3	± 54.5	—	—	—	—
N			742	724	625	433	247	113	41	13	3	1	1	1	1
Annual increment			124.9	119.4	75.3	54.1	41.8	20.7	16.7	5.8	44.2	6.6	4.3	13.0	8.6

TABLE 6.—Back-calculated fork lengths (mm) at age for female gray triggerfish from the northeastern Gulf of Mexico, 1979-82.

Age group	Mean length ± 1SD at capture	N	Average back-calculated FL at age											
			1	2	3	4	5	6	7	8	9	10	11	12
I	259.0 ± 34.0	12	155.6											
II	300.4 ± 35.2	93	120.1	241.4										
III	330.8 ± 46.2	187	117.0	227.8	298.3									
IV	360.1 ± 57.5	161	117.9	226.3	292.4	335.6								
V	398.5 ± 64.0	85	128.2	226.5	291.7	340.7	378.5							
VI	402.5 ± 63.6	55	113.5	218.4	276.0	320.1	357.5	387.1						
VII	419.8 ± 73.6	16	124.9	205.3	260.9	307.2	345.9	379.0	405.1					
VIII	448.8 ± 79.6	5	109.0	193.3	262.3	305.7	342.4	376.8	415.1	437.4				
IX	457.8 ± 71.2	10	101.8	208.1	264.8	306.9	340.2	373.7	402.5	431.0	447.9			
XII	561.0 ± —	1	121.2	258.2	390.4	463.2	481.2	494.6	516.8	525.7	534.6	547.8	552.2	556.6
Weighted mean			119.4	227.3	291.1	332.0	366.1	384.7	409.3	438.9	455.8	547.8	552.2	556.6
± 1SD			± 37.8	± 43.1	± 45.1	± 53.3	± 61.1	± 62.4	± 70.0	± 71.4	± 73.6	—	—	—
N			625	613	520	333	172	87	32	16	11	1	1	1
Annual increment			119.4	107.9	63.8	40.9	34.1	18.6	24.6	29.6	16.9	92.0	4.4	4.4

TABLE 7.—Back-calculated fork lengths (mm) at age for all gray triggerfish collected from the northeastern Gulf of Mexico, 1979-82.

Age group	Mean length ± 1SD at capture	N	Average back-calculated FL at age												
			1	2	3	4	5	6	7	8	9	10	11	12	13
I	259.3 ± 29.7	34	140.9												
II	308.6 ± 42.3	210	121.7	247.4											
III	343.9 ± 52.1	424	118.0	235.4	308.9										
IV	384.0 ± 66.1	398	122.0	235.3	307.3	356.1									
V	425.8 ± 70.7	243	128.1	236.6	309.1	361.8	403.9								
VI	434.7 ± 67.1	141	123.9	232.6	295.0	346.0	386.6	417.7							
VII	541.0 ± 64.6	49	123.6	221.0	286.7	334.8	373.2	409.0	435.7						
VIII	464.8 ± 54.2	16	134.2	227.1	296.3	335.3	372.2	401.3	432.6	452.2					
IX	478.1 ± 72.3	14	117.4	233.5	282.6	324.1	354.4	388.8	420.1	448.4	468.6				
X	439.0 ± —	1	108.3	204.0	251.5	274.8	286.3	309.2	331.9	354.9	384.1	420.8			
XII	561.0 ± —	1	212.2	258.2	390.4	463.2	481.2	494.6	516.8	525.7	534.6	547.8	552.2	556.6	
XIII	544.0 ± —	1	91.9	308.4	395.0	452.7	461.5	479.0	492.1	496.5	500.8	509.5	513.8	526.7	535.4
Weighted mean			112.8	236.5	305.8	354.1	392.9	412.9	432.8	451.2	460.4	492.7	533.0	541.7	535.4
± 1SD			± 40.0	± 47.8	± 52.6	± 61.0	± 65.9	± 66.0	± 64.0	± 61.8	± 72.0	± 65.1	± 27.2	± 21.1	—
N			1,523	1,498	1,288	864	466	223	82	33	17	3	2	2	1
Annual increment			112.8	123.7	69.3	48.3	38.8	20.0	19.9	18.4	9.2	32.3	40.3	8.7	−6.3

all fish $W = 2.146 \times 10^{-5} L^{2.992}$, $r = 0.96$, $n = 175$.

Conversions between different length measures were linear and expressed as follows:

FL vs. TL: FL = 29.704 + 0.774 TL, r = 0.97, n = 100,

FL vs. SL: FL = 22.823 + 1.171 SL, r = 0.99, n = 100,

TL vs. SL: TL = 9.666 + 1.446 SL, r = 0.96, n = 100.

Estimates of mortality (a, s, and i) varied slightly between estimation methods (Table 8). Full recruitment to the fishery was considered to be at 3 yr for both sexes. Estimates of a were between 0.32 and 0.53 with i between 0.39 and 0.75 (Table 8).

TABLE 8.—Estimated annual mortality (a), annual survival (s), and instantaneous mortality (i) by estimation technique for gray triggerfish from the northeastern Gulf of Mexico, 1979-82.

	Estimation technique			
	Heincke (1913)	Jackson (1939)	Robson and Chapman (1961)	Regression analysis
Males				
a	0.33	0.32	0.44	0.53
s	0.67	0.67	0.56	0.47
i	0.40	0.39	0.57	0.75
Females				
a	0.36	0.32	0.45	0.47
s	0.64	0.68	0.55	0.53
i	0.45	0.38	0.59	0.64
All fish				
a	0.34	0.33	0.44	0.49
s	0.66	0.64	0.56	0.51
i	0.41	0.40	0.58	0.67

DISCUSSION

The variation in length at age and overlays of length ranges between ages found in gray triggerfish is not unusual in fish from southeastern U.S. waters. Many species such as king mackerel, *Scomberomorus cavalla*; Spanish mackerel, *S. maculatus*; red grouper, *Epinephelus morio*; sailfish, *Istiophorus platypterus*; and black sea bass, *Centropristis striata*, have large variations in size within age groups (Beaumariage 1973; Powell 1975; Moe 1969; Jolley 1977; Waltz et al. 1979).

Our gray triggerfish growth rates are similar to growth information from the Gulf of Mexico, but not information from Africa. Beaumariage (1969) reported growth rates for three tagged fish (250, 270, and 332 mm TL) from the northeastern Gulf of Mexico. His fish grew at a rate of 187.2, 153.6, and 51.6 mm/yr. If one considers Beaumariage's fish to be 2, 2, and 3 yr old, respectively, then his growth increments are similar to ours (Table 7). Gray triggerfish age and growth have been reported from southwestern Africa (Ivory Coast-Ghana-Togo area) by Anonymous (1980). We took the information in Anonymous' figure 11 and converted it to mean length at capture per age which gave the following approximate values: age I, 148 mm; age II, 203 mm; values are about 100 mm less than ours for each age (Table 7). Caveriviere et al. (1981) provided comprehensive information on the age and growth of gray triggerfish off Senegal and the Ivory Coast. Two hypotheses with regard to band formation were suggested: A) one band per year, and B) two bands per year. The sizes (FL) at age (in years) for Senegal fish by hypotheses were age I, 153 mm for hypothesis A, 90 mm for B; age II, 231 mm for A, 170 mm for B; age III, 285 mm for A, 238 mm for B; age IV, 322 mm for A, 290 mm for B; age V, 348 mm for A, 324 mm for B. Sizes at age of our Gulf of Mexico fishes (Table 7) were larger after the first year than predicted by both of the above hypotheses for Senegal fish. The sizes at age for Ivory Coast fish were smaller than both the Senegal and the Gulf of Mexico fish using the hypothesis of one band formed per year. These differences may be the result of different environments, biology, methods of capture, or aging. Anonymous (1980) suggested that the African fish have a seasonal offshore migration to avoid the cold coastal water (during the third quarter of the year) which is the result of upwelling. Gulf of Mexico fish are not known to have migratory habits, and thus might not be subject to the energy expense such movements incur. More information on the life histories and environments of these groups of gray triggerfish is needed to explain the observed variations.

The K values (growth coefficient) of gray triggerfish varied between 0.382 and 0.383. These values were similar to, but higher (about 0.1) than, those reported for other demersal marine fish from the southeastern United States (see Manooch 1982 and Pauly 1978 for a listing of values). The K values estimated for gray triggerfish may be high because of the low asymptotic lengths that were found. Additional investigation of the larger and older fish is needed to evaluate the growth coefficients of this species. The esti-

mates of mortality (Table 8) were similar to those of demersal marine fish such as the white grunt, *Haemulon plumieri*, where a = 0.37-0.51 and the red porgy, *Pagrus pagrus*, where a = 0.32-0.55 (Manooch 1976; Manooch and Huntsman 1977) that inhabit similar habitats. The mortality rates for gray triggerfish probably reflected the exploitation level on this species in the northeast Gulf of Mexico. Nelson and Manooch (1982) reported similar values (i = 0.39-0.50) for red snapper, *Lutjanus campechanus*, from the Carolinas and Florida coasts where the fishing pressure is light to medium and much higher values (i = 0.78-0.94) from the fishery off Louisiana where the commercial fishing pressure is high. The effect of fishing on gray triggerfish populations were therefore assumed to be similar to the effects of fishing on these other reef fish resources.

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THE EFFECT OF DISTURBANCE ON HARBOR SEAL HAUL OUT PATTERNS AT BOLINAS LAGOON, CALIFORNIA[1]

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ABSTRACT

We studied harbor seals at Bolinas Lagoon, California, from May 1978 to June 1979. Field observation and two time lapse motion picture cameras were used to monitor the numbers of seals and of disturbances, and to provide information on tidal height. Peak numbers occurred during the summer. During nonbreeding seasons, high numbers occurred at low tides, and during the breeding season they occurred in early afternoon except when haul out areas were flooded. Seals were disturbed by humans on 71% of days monitored; people in canoes were the primary source of disturbance. Human activities closer than 100 m caused seals to leave haul out sites more than activities at greater distances.

Several studies exist on the haul out patterns of harbor seals, *Phoca vitulina*, in undisturbed locations (Scheffer and Slip 1944; Venables and Venables 1955; Richardson 1975[4]; Pitcher 1977[5]; Loughlin 1978), but the effects of human activities on haul out patterns have been examined infrequently (Newby 1971; Paulbitsky 1975; Chapman 1979[6]). We report here how daily and seasonal haul out patterns of harbor seals can be modified by human activity in a small estuary, Bolinas Lagoon, Calif. The data also provide a baseline against which the effects of pending increased levels of human activity could be compared.

Since 1970, a state quarantine has reduced human activities in the contaminated waters of Bolinas Lagoon. Human use has been confined to bird watching, some boating, illegal clam digging, beach combing, and recreational bait fishing. When the quarantine is lifted, many of these activities will increase. Increased human activity could also result from provisions included in the General Management Plan of the Golden Gate National Recreation Area (June 1979) for a walk-in camp site and parking area along the lagoon.

Little information exists on harbor seals at Bolinas Lagoon. Carlisle and Alpin (1966, 1971) estimated numbers as part of a statewide aerial count, but their figures for Marin County were low compared with preliminary data collected by Gary W. Page (unpubl. data). More recently, Mate's (1977)[7] monthly statewide counts failed to detect any seals in Bolinas Lagoon.

STUDY AREA AND METHODS

Bolinas Lagoon, a 448 ha estuary 24 km north of San Francisco, is a Marin County Nature Preserve and is part of the Golden Gate National Recreation Area. Triangular in shape, it is bordered by paved roads, pasture land, the small community of Bolinas, and a 3 km long sand spit covered with houses. At the end of the spit there is a 60 m wide opening to the ocean. The major channel used by the seals passes by Kent Island (KI) and Pickleweed Island (PWI) and cuts north along the northeastern shore (Fig. 1). KI and PWI remain above water when tides exceed 1.7 m above mean low water level and are the two main seal haul out areas.

Movie cameras recorded the activity of seals and humans in the vicinity of KI and PWI. A Canon[8]

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[8]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

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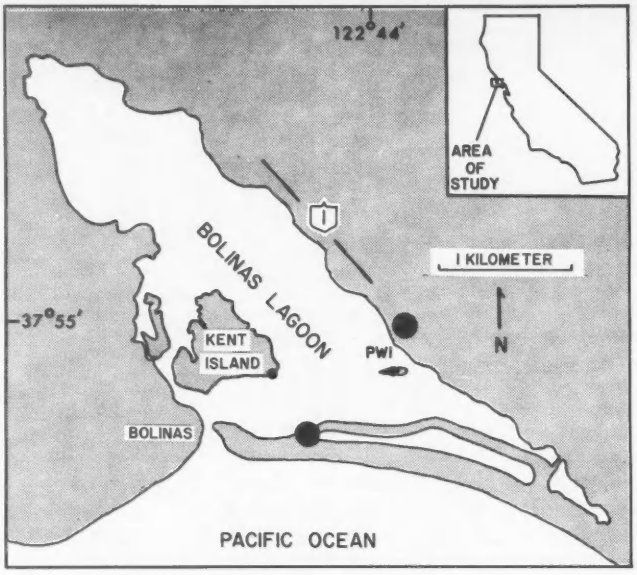

FIGURE 1.—Study area showing the two major haul out sites, Kent Island (KI) and Pickleweed Island (PWI), Calif., (small solid circles), and the location of the two cameras (large solid circles).

"814 XL Super 8" with a 7.5 to 60 mm zoom lens was focused on KI from a private residence on the sand spit about 400 m away. A photocell activated the camera at day break and deactivated it at sundown; an intervalometer exposed one frame of film every minute. Another camera, a Eumig "880 Super 8" with a 7 to 56 mm zoom lens, positioned in a weatherproof box on private property along State Route 1, was focused on PWI, about 300 m away. The built-in intervalometer also triggered 1 frame/min. An electrical timer activated the camera during daylight hours. The film used (Kodachrome ASA 40) contained 3,000 frames/roll and lasted a week except during summer, when film was changed every 4 d due to increased day length.

We used a Kodak "Moviedeck model 475" projector to analyze film. We noted time, tide level, and the number of seals once every hour of photographic time. Any major change in seal numbers within the 1 h interval was also noted, as well as any disturbance. A stake marked with 0.3 m increments was placed near the major channel by KI and in line of the Canon's viewfinder. This provided a photographic record of tidal change. Actual time for the first frame each day was extrapolated from tables for sunrise and sunset; on several mornings and evenings we compared these times with the actual time that camera operation began or ceased. Extrapolated times were accurate to within 1.0 h.

Twelve (once per month) day-long watches and 211 (124 breeding, 47 summer, and 40 winter) incidental sightings validated camera counts, detected sources of disturbance outside the camera field, estimated disturbance distance from the herd, identified additional haul out sites, and accurately counted pups, which were difficult to detect on film.

When analyzing data, the year was divided into three seasons: winter (November through February), breeding (March through June), and summer (July through October); seasonal averages are expressed with ± 1 standard deviation. Correlation coefficients were calculated to compare camera and field counts as a test for camera reliability, and to examine the relationship of seal numbers to tide level within each hour (Snedecor and Cochran 1967). For daily use per season graphs of hourly means were compared; the "runs up and down test" (Bradley 1968) was used to test the sequence of hourly means for randomness.

All human activities (including dogs off leashes) in the area were divided into two types: actual disturbance and zero-seal disturbance. Actual disturbances, or any activity occurring when at least one seal was present, were further subdivided into type I, where at least one seal left the area, and

type II, where no seals left the area. A zero-seal disturbance was any activity occurring in the area when seals were not hauled out but which may have prevented seals from doing so.

To investigate the effect of actual disturbance on the seals at KI, disturbances were classified by four criteria: 1) seal response (yes, at least one seal left; no, no seals left); 2) distance between the seals and the disturbance source (≤100 m, 101-200 m, 201-300 m); 3) day of week (weekend/holiday, weekday); and 4) disturbance type (person/dog, nonpower boat, power boat). Due to the low number of disturbances during the breeding and winter seasons, season was not used as a variable. Only the 156 instances where disturbance type and distances were known were used in the analysis. The result was a $2 \times 3 \times 2 \times 3$ contingency table. We used log-linear models to examine the effects of 2, 3, and 4 (explanatory variables) on 1 (response variable). Log-linear models are used to analyze multidimensional contingency tables and can be used to study two- and three-way interactions between variables (Bishop et al. 1975). We asked the question: "Is seal response independent of the other variables?" We then asked: "If not, what variables affect seal response?" Exploration of models was done by backward and forward selection of models (models were fit with iterative proportional fitting). Both methods produced the same final model; only the backward selection method is presented in the paper.

Backward selection starts with a model that fits the data. All interaction terms that are found to be not significantly different from zero by using a conditional likelihood ratio test (Fienberg 1981) are removed from the model. The final model is found when all nonsignificant terms are deleted. Models were adjusted for marginal zeros (Bishop et al. 1975: Ch. 3), and are displayed here using a shorthand notation (Fienberg 1981). For example, seal response independent of all other variables is denoted [1] [234], and seal response dependent on one of the variables, such as distance, is denoted [12] [234]. Once the final model is selected, weights or "u-terms" are calculated from the data, and are given to each of the levels of each variable included in the final model. The sign of the weight indicates the effect of the explanatory variable [2, 3, or 4] on the response variable [1]. The relative magnitude of the weight indicates the importance of the explanatory variable.

The average time it took for seals to recover from disturbance was based on the elapsed time between when the seals were flushed to when 50% of the original number had rehauled. A chi-square test determined the significance of tide level on the ability of seals to recover from disturbance at KI (Snedecor and Cochran 1967). Correlation coefficients were used to detect the importance of PWI as an alternate haul out site.

RESULTS

Camera Reliability

A correlation of KI camera counts with field counts revealed that the camera was not a reliable indicator of the actual number of seals present but was reliable for information on daily trends. Correlation coefficients by season were as follows: winter, $r = 0.92$, $n = 19$; breeding, $r = 0.55$, $n = 40$; summer, $r = 0.75$, $n = 28$. Discrepancies between the two count methods were caused by seals shifting along the haul out area and, therefore, out of the camera's viewfinder, the inclination of females with pups to haul out on the fringe of the herd, and the difficulty in identifying pups. On the other hand, the camera was very reliable at PWI for the summer ($r = 0.94$, $n = 25$) and breeding ($r = 0.97$, $n = 13$) seasons because seals could not shift out of viewfinder range. Also, this camera was slightly elevated, allowing for better detection of seals hauled out close together. During much of the winter season the PWI camera was broken. Both cameras readily detected boats and people on foot disturbing seals, but could not detect aircraft. Dogs were seen on film twice and on 13 occasions during field counts.

Seasonal and Spatial Use Patterns

Seals used the lagoon on 95-100% of the days each month. More seals hauled out on KI during the breeding and summer seasons than during winter. Numbers on field counts averaged 31.2 ± 28.1 seals during the breeding season (range 0-101, $n = 78$), 53.5 ± 28.5 during the summer (range 0-105, $n = 48$), and 19.6 ± 19.3 during the winter (range 0-58, $n = 28$). The same trend was apparent from field counts on PWI; the number of seals averaged 10.6 ± 15.1 for the breeding season (range 0-77, $n = 107$), 10.0 ± 18.4 for summer (range 0-48, $n = 41$), and 7.7 ± 12.5 for winter (range 0-55, $n = 43$). The PWI means were much lower than those for KI, indicating that KI was the preferred haul out site.

During the breeding season, mother-pup pairs hauled out on PWI and on exposed sand bars along

the major channel, but on 83% (125 d) of 150 camera monitoring days, seals were present on KI. Ten and 12 pups were counted in 1978 and 1979, respectively. After the breeding season in July, seals were present on 97% (111 d) of 114 camera days. By contrast, seals were counted on PWI on 56% (54 d) of 96 camera census days during the breeding season and 73% (74 d) of 102 d in the summer. After October, when the population declined, the level of use was still high at KI with seals present on 81 of 92 camera census days.

Daily Use

Peak numbers of seals usually occurred in early afternoon at both sites except at KI during winter when a constant number were present until late afternoon (Table 1, Figs. 2, 3). All the daily trends were significantly different from randomness except for PWI during winter [$P = 0.02$ for KI winter, $P = 0.008$ for KI breeding, $P = 0.007$ for KI summer; $0.24 < P < 0.06$ for PWI winter, and $P < 0.001$ for PWI breeding and summer ("runs up and down test")]. The greater use of KI during the summer and breeding seasons is also reflected in the elevated hourly means (Fig. 2).

Correlation coefficients revealed a positive correlation between low tides and seal numbers (Table 2). The daily temporal use pattern (Table 1) was affected by tide level during winter (range of $r = 0.54 - 0.75$) and summer (range of $r = 0.49 - 0.69$) for KI and to a lesser extent during the summer for PWI (range of $r = 0.11 - 0.62$). No tidal effect was apparent at either site during the breeding season.

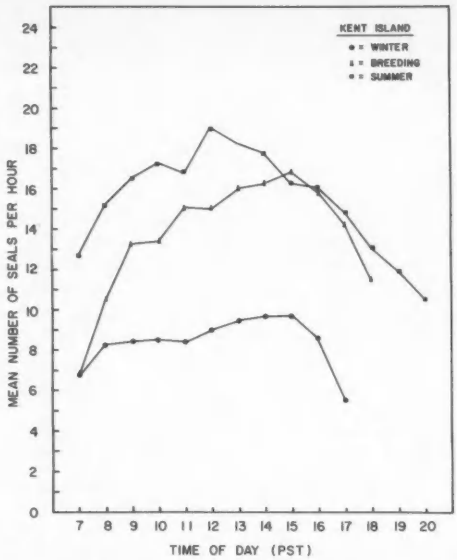

FIGURE 2.—Graph of time of day and the mean number of seals hauled out per time period for winter, breeding, and summer seasons at Kent Island.

Disturbance

Camera and field observations of KI recorded 539 actual and zero-seal disturbances. Of those with identifiable cause, 33.1% were nonpower boats, 10.0% people on foot, 7.8% power boats, 3.4% clam diggers or bait harvesters, 2.8% dogs, and

TABLE 1.—The relationship between time of day and the number of seals hauled out per season on Kent Island (KI) and Pickleweed Island (PWI); $\bar{x}$ is the mean number of seals per hour, SD is the standard deviation, and n is the sample size.

		Time													
Season		0700	0800	0900	1000	1100	1200	1300	1400	1500	1600	1700	1800	1900	2000
Winter															
KI	$\bar{x}$	6.8	8.3	8.4	8.5	8.4	9.0	9.5	9.8	9.8	8.7	5.6			
	SD	9.5	11.6	11.9	11.6	11.7	11.4	12.0	12.5	12.0	11.5	8.9			
	n	84	83	84	84	87	88	87	88	87	87	12			
PWI	$\bar{x}$	0	0.8	3.5	6.9	6.3	5.5	6.2	5.4	2.2	2.2				
	SD	0	2.1	4.9	6.7	6.2	6.6	6.8	6.0	3.9	3.6				
	n	9	8	10	10	11	11	10	10	10	10				
Breeding															
KI	$\bar{x}$	6.9	10.6	13.3	13.4	15.1	15.1	16.1	16.4	16.9	15.9	14.3	11.6		
	SD	10.2	13.8	16.5	16.0	16.8	16.3	16.8	16.1	16.5	16.2	15.3	13.8		
	n	105	108	112	114	118	119	118	119	116	116	116	94		
PWI	$\bar{x}$	1.2	1.9	2.6	3.3	4.0	4.2	4.7	4.9	4.9	3.8	3.3	0.1		
	SD	3.1	4.8	5.8	6.6	7.3	8.0	8.3	8.4	8.5	7.3	6.5	0.3		
	n	87	89	86	89	91	89	92	91	91	90	83	37		
Summer															
KI	$\bar{x}$	12.7	15.2	16.5	17.3	16.8	19.1	18.3	17.8	16.4	16.1	14.8	13.1	12.0	10.6
	SD	14.4	15.9	17.4	17.7	16.5	18.0	18.2	18.2	17.8	16.8	15.3	14.9	15.1	15.3
	n	77	83	92	98	104	102	101	105	105	103	86	51	27	
PWI	$\bar{x}$	0.4	1.2	2.1	3.5	4.7	5.4	5.0	4.5	3.6	2.4	1.3	0.8	0.6	0.7
	SD	1.0	4.0	5.5	9.2	10.8	12.0	12.8	11.1	10.6	7.4	3.9	3.0	2.5	2.2
	n	91	90	91	94	101	101	99	99	98	98	98	92	70	14

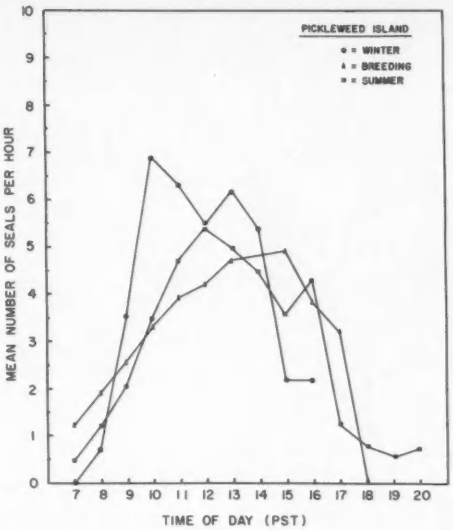

FIGURE 3.—Graph of time of day and the mean number of seals hauled out per time period for winter, breeding, and summer seasons at Pickleweed Island.

0.7% helicopters. The camera did not record the cause in 40% of the disturbances. During December, January, and February, commercial bait harvesters accounted for 25.7% of the disturbances. Disturbances from aircraft were detected only in field observations. The seals were disturbed at least once on 71% of 356 d when the KI camera was functioning, and during these days, 72.7% of 539 disturbances caused the seals to disperse (Table 3). On 211 d during which the PWI camera was functional, seals reacted to 57% of 236 disturbances (Table 3). The frequency of actual disturbances per day averaged highest during the summer for both KI and PWI.

Of the actual disturbances of known cause, most occurred within 100 m of the KI site and resulted more from nonpower boats than from any other source (Table 4). The deletion of terms [13] and [14] from the log-linear model in backward selection, however, indicated that only the distance of a disturbance significantly affected seal behavior (Table 5). Seals did not react differentially to any disturbance type and did not react more to disturbances during weekend/holidays than during weekdays. The relative magnitude of the weights associated with the distance/seal response interaction term [12] denoted that seals responded to

TABLE 2.—Correlation coefficients between tide level and the number of seals hauled out at hourly intervals per season at Kent Island (KI) and at Pickleweed Island (PWI), from camera data; n = number of censuses. Insufficient data were available for PWI during the winter. A positive correlation indicates a positive relationship between seal number and low tide, and a negative correlation indicates a negative relationship between seal number and high tide.

	Winter	Breeding		Summer	
Time	KI (n = 27)	KI (n = 26)	PWI (n = 16)	KI (n = 24)	PWI (n = 21)
0800	0.54**	0.35	0.23	0.49**	0.36
0900	0.75**	0.34	0.17	0.69**	0.20
1000	0.67**	0.42*	−0.17	0.55**	0.62**
1100	0.71**	0.31	−0.30	0.57**	0.52**
1200	0.64**	0.14	0.06	0.68**	0.48*
1300	0.65**	−0.12	0.34	0.54**	0.45*
1400	0.58**	−0.15	0.42	0.62**	0.37
1500	0.55**	0.001	0.22	0.67**	0.23
1600		0.20	0.11	0.67**	0.11

* Significant at $P = 0.05$.
**Significant at $P = 0.01$.

TABLE 3.—The frequency of disturbances on Kent Island (KI) and Pickleweed Island (PWI) by season; n is the number of days the camera was functional, A is the number of actual and zero-seal disturbances combined, $A1$ is the number of actual disturbances type I, A/n is the mean number of all disturbances per day, and $A1/n$ is the mean number of the actual disturbances per day.

	KI					PWI				
Season	n	A	$A1$	A/n	$A1/n$	n	A	$A1$	A/n	$A1/n$
Breeding	150	216	158	1.4	1.1	96	101	54	1.1	0.6
Summer	114	215	167	1.9	1.5	102	121	75	1.2	0.7
Winter	92	108	67	1.2	0.7	13	14	6	1.1	0.5
Totals	356	539	392	1.5	1.1	211	236	135	1.1	0.6

TABLE 4.—Data from the Kent Island camera used in log-linear model analysis (Bishop et al. 1975). The numbers in the table are the number of disturbances where seals were present for each category. Y = response (at least one seal left site); N = no response (no seals left site).

	Weekday						Weekend/holiday					
Distance:	<100 m		101-200 m		201-300+ m		<100 m		101-200 m		201-300+ m	
	Y	N	Y	N	Y	N	Y	N	Y	N	Y	N
People/dog	12	0	1	0	0	0	12	0	2	0	0	0
Nonpower boat	35	2	8	5	1	7	32	1	5	1	1	6
Power boat	7	1	3	3	1	0	8	0	0	1	1	0

TABLE 5.—Backward selection of log-linear model using data in Table 4; model variables are 1 (response), 2 (distance), 3 (day of week), and 4 (disturbance type). An asterisk indicates a term that is significantly different from zero.

Model	G	df	P	Term deleted
[12] [13] [14] [234]	11.15	8	>0.10	
[12] [13] [234]	15.4	13	>0.25	[14]
[12] [14] [234]	12.18	9	>0.25	[13]
[13] [14] [234]	57.52	14	<0.01	[12] *
[12] [234]	16.91	14	>0.25	[14]
[14] [234]	58.98	11	<0.01	[12] *
[1] [234]	70.38	18	<0.01	[12] *

Final model = [12] [234]

disturbances at ≤100 m more than at distances 101-200 m and 201-300 m, and were least reactive to disturbances at 201-300 m (Table 6).

TABLE 6.—Weights associated with the distance/seal response interaction term [12] of the log-linear model that fits the data in Table 5. Relative magnitude of weight indicates importance of the variable. Sign of the weight indicates direction of effect (+ is more, − is less).

Distance (m)	Seal response	
	Yes	No
0-100	[1]1.116	−1.116
101-200	−0.201	0.201
201-300	−0.915	[2]0.915

[1]Seals were most reactive to disturbance.
[2]Seals were least reactive to disturbance.

After actual disturbances (type I), the number of seals that eventually rehauled was always lower than the original number. On KI, the average time it took seals to rehaul regardless of season, was 28 ± 20.8 min (range 5-100, $n = 187$). In 96 instances, no seals rehauled, primarily due to tidal height. During rising tides, they rehauled only 16.2% of the time ($n = 37$ disturbances), at low slack tide, 55.6% of the time ($n = 124$), and on falling tides 61.5% of the time ($n = 26$; $\chi^2 = 13.82, P < 0.001$).

Disturbances were of short duration and seals rehauled after the disturbance source had left the area, except for disturbance from commercial bait harvesters, who remained in the vicinity for entire low tide cycles. Bait harvesters likely prevented seals from hauling out at all (zero-seal disturbance). During December, January, and February, we recorded the presence of the harvesters on 13 d. After being disturbed, seals did not return to the haul out site on eight of those days. They were disturbed briefly by the harvesters and then rehauled on 3 d, and there was no change in seal numbers on 2 d.

PWI apparently was not an important alternative site when KI was disturbed. A weak correlation between seal numbers at PWI after they were disturbed from KI existed during the winter ($r = -0.42, n = 7$) and summer ($r = -0.40, n = 152$), but not during the breeding season ($r = -0.14, n = 123$). In 45 of these instances, however, (winter 3, breeding 14, and summer 28), disturbances occurred simultaneously at KI and PWI, thereby precluding seal movement to PWI. During field observations, the movement from KI to PWI after disturbance was actually observed on 11 occasions.

DISCUSSION

The population of harbor seals at Bolinas Lagoon is much higher than previously recognized, and in contrast to seasonal peaks during the breeding season at other seal haul out sites (Fancher 1979; Johnson and Jeffries 1977[9]; Loughlin 1978; and Allen and Huber 1983[10]), the peak at Bolinas Lagoon occurred during summer after the pupping season. The peak at Bolinas may be caused in part by an influx of seals, possibly from San Francisco Bay, only 24 km south, or from Double Point, 10 km north, where numbers decline after the pupping season (Risebrough et al. 1978[11]; Allen and Huber 1983 footnote 9). The summer increase also coincides with a marked increase in fish abundance in Bolinas Lagoon and Bolinas Bay; fish abundance and species diversity are greater in the lagoon from May to September than from November to February (J. Gustafson[12]). Scheffer and Sperry (1931), Spalding (1964), and Pitcher (1977 footnote 5), suggested that harbor seals are opportunistic, preying primarily upon small schooling fish. In a study by Brown and Mate (1983), peak abundance of seals in Netarts Bay, Oreg., also occurred in the fall and coincided with the seasonal abundance of chum salmon. Movement to Bolinas Lagoon at a time of high food availability may be a consequence of the seal's opportunistic feeding strategy.

Time of day and tide were important factors that influenced daily haul out patterns of seals. The peak in numbers during early afternoon is consistent with studies on the Farallon Islands (Ainley et al. 1977[13]) and in San Francisco Bay (Fancher 1979). Though seals were seen hauled out on KI at night on 10 occasions, the sharp drop in numbers during late afternoon suggests that diurnal hauling out is preferred. The diurnal pattern may also

[9]Johnson, M. L., and S. J. Jeffries. 1977. Population evaluation of the harbor seal (*Phoca vitulina richardi*) in the waters of the State of Washington. U.S. Dep. Commer., N.T.I.S. PB-270 376, 27 p.

[10]Allen, S. G., and H. R. Huber. 1983. Pinniped assessment in the Point Reyes/Farallon Islands National Marine Sanctuary, 1982-83. Annual Report to U.S. Department of Commerce, Sanctuary Programs Office, 64 p.

[11]Risebrough, R. W., D. Alcorn, S. G. Allen, V. C. Alderlini, L. Booren, R. L. DeLong, L. E. Fancher, R. E. Jones, S. M. McGinnis, and T. T. Schmidt. 1978. Population biology of harbor seals in San Francisco Bay, California. U.S. Dep. Commer., N.T.I.S. PB81-107963, 67 p.

[12]J. Gustafson, Environmental Consultant, Resources and Ecology Projects, Mill Valley, CA 94941, pers. commun. August 1979.

[13]Ainley, D. G., H. R. Huber, R. P. Henderson, T. J. Lewis, and S. H. Morrell. 1977. Studies of marine mammals at the Farallon Islands, California, 1975-76. U.S. Dep. Commer., N.T.I.S. PB-266 249, 32 p.

be related to seal feeding habits as discussed by Antonelis and Fiscus (1980) and Spalding (1964) who noted that seals fed primarily in the late afternoon. The weak inverse correlation between tide level and seal numbers during the breeding season is likely related to the tendency of females with pups to haul out at irregular times to nurse.

These patterns were interrupted by disturbance from boats, pedestrians, dogs, and aircraft. People in nonpower boats were the greatest source for disturbance possibly because they are more mobile than people in power boats or on foot. Distance of disturbance, however, rather than type or season was the significant element at KI since at distances >100 m seals tended not to leave the hauling out site. The response of seals at distances >100 m may have been precipitated by the nature or unpredictability of the disturbance source. For example, a boat advancing directly toward the seals or lingering nearby caused flight more often than a boat moving by.

The source of current disturbances is a small but stable resident and tourist human population; however, a variety of changes in the seal's behavior may be expected if disturbance levels increase. Both Paulbitsky (1975) and Woodhouse[14] documented a change from diurnal to nocturnal hauling out patterns in seals at Strawberry Spit, Tiburon, and at Atascadero State Beach, Morro Bay, Calif., which was believed to be a response to an increase in the local human populations. The response of seals to the prolonged activities of commercial bait harvesters on Bolinas Lagoon is indicative of the potential disruption of seal haul out patterns.

Excessive disturbance may also lead to increased pup mortality. According to Kenyon (1972), 7 of 18 Hawaiian monk seals, *Monachus schaunislandi*, died before weaning on heavily disturbed pupping grounds on Midway Atoll, Hawaii. In contrast, for harbor seals at a relatively undisturbed pupping ground in British Columbia, Bigg (1969) estimated that pup mortality was only 12%. We do not know to what extent disturbance is affecting pup mortality rates at Bolinas Lagoon. In 1979, 3 of 12 pups were found dead; at least 1 of those 3 was killed by a dog.

Site abandonment is a third possible response to increased disturbance. Newby (1971) attributed harbor seal abandonment of a site in Puget Sound in part to increased disturbance from recreational boating. Kenyon (1972) postulated for the monk seal that site abandonment results in overall population losses because other traditional haul out sites probably cannot absorb the emigration. The same could apply to harbor seal populations in Marin County, if other sites are currently filled to capacity.

[14]C. Woodhouse, Santa Barbara Museum of Natural History, 2559 Puesta del Sol, Santa Barbara, CA 93105, pers. commun. May 1977.

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REPRODUCTION OF WEAKFISH, *CYNOSCION REGALIS*, IN THE NEW YORK BIGHT AND EVIDENCE FOR GEOGRAPHICALLY SPECIFIC LIFE HISTORY CHARACTERISTICS

GARY R. SHEPHERD[1] AND CHURCHILL B. GRIMES[2]

ABSTRACT

Reproduction characteristics for weakfish, *Cynoscion regalis*, in the New York Bight were examined. Spawning in 1980-81 occurred from May to early July with spawning time dependent on parental size. Maturity for both sexes occurred by age 1 but at a greater size in females. Annual fecundity estimates were compared with literature values for North Carolina weakfish and were found to be considerably lower at size, yet cumulative fecundities were nearly equivalent. The latitudinal variations in fecundity may be a behaviorally and environmentally induced phenomena, and influence the long-term population stability of weakfish.

Weakfish, *Cynoscion regalis*, are a member of the family Sciaenidae and are a common inshore species occurring between Cape Cod, Mass., and southern Florida. The species undergoes a spring migration from offshore waters of Virginia and the Carolinas to appropriate estuarine spawning areas, then a return migration in late fall to overwintering grounds (Nesbit 1954). The center of greatest abundance occurs within the Middle Atlantic Bight in quantities sufficient to support a recreational and commercial fishery. In 1979 commercial fishermen landed 13,000 metric tons (t) of weakfish and nearly 5,000 t were caught by recreational anglers (Wilk 1981). Abundance has, however, undergone some dramatic fluctuations over the last several decades. Commercial landings averaged 8,800 t from 1940 to 1949, then dropped to 2,915 t by 1950, and remained at these low levels until the mid-1970's (Wilk 1981). The exact cause of these variations remains a mystery, although speculations include overfishing, DDT-induced mortality, and environmentally induced recruitment failure (Massman 1963; Joseph 1972; Merriner 1976). To adequately assess the mechanisms controlling recruitment success or failure, we must first have a thorough understanding of the reproductive biology of weakfish.

Merriner (1976) has examined reproduction of weakfish in North Carolina, and Daiber (1957) mentioned spawning behavior of weakfish in Delaware Bay, but the reproductive biology of weakfish in their northern range has never been fully investigated. Furthermore, there is reason to believe that reproduction may vary throughout the geographic range. Leggett and Carscadden (1978) have shown latitudinal variations in reproduction and growth of American shad, *Alosa sapidissima*, and White and Chittenden (1977) have likewise shown geographic differences in another sciaenid, the Atlantic croaker, *Micropogonias undulatus*. Growth differences have already been established for weakfish between the New York Bight and North Carolina (Perlmutter et al. 1956; Shepherd and Grimes 1983), so there is reason to suspect possible reproductive differences. The purpose of the study was to investigate weakfish reproduction in the Middle Atlantic region, to determine if any geographic variations exist, and to consider possible reasons for geographically specific characteristics.

METHODS AND MATERIALS

Sample Collection

Samples (n = 1,208) were collected during the National Marine Fisheries Service (NMFS) groundfish survey from 1980 to 1983 at stratified random stations north of Chesapeake Bay (Fig. 1). Fish were collected with a #41 Yankee trawl in spring and a #30 Yankee trawl in summer and fall at depths between 5 and 200 m (Grosslein 1969). NMFS samples were supplemented by 461 fish collected between May 1980 and June 1981 from commercial pound nets in Gardiners Bay, N.Y., (n = 61) and Sandy Hook Bay, N.J., (n = 115) and

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from pair and otter trawl fisheries in Delaware Bay (n = 285).

At each NMFS station, weakfish catches were stratified into 10 cm size intervals and 10-15 fish sampled per interval. Total length to the nearest centimeter, sex, and maturity stage were recorded. Weakfish from Gardiners Bay were randomly sampled, total length measured to the nearest millimeter, sex, and maturity stage recorded, and gonads removed and weighed to the nearest 0.1 g. Sandy Hook and Delaware Bay samples were collected by random selection of 50-lb (22.5 kg) boxes in each market category available from the catch, and total length to the nearest millimeter and weight (whole and gutted) to the nearest gram recorded. Gonads and livers were also removed and weighed to the nearest 0.1 g. Gonads were preserved in modified Gilson's solution (Bagenal and Braum 1971) for several weeks, then removed, washed with distilled water and stored in 95% isopropyl alcohol.

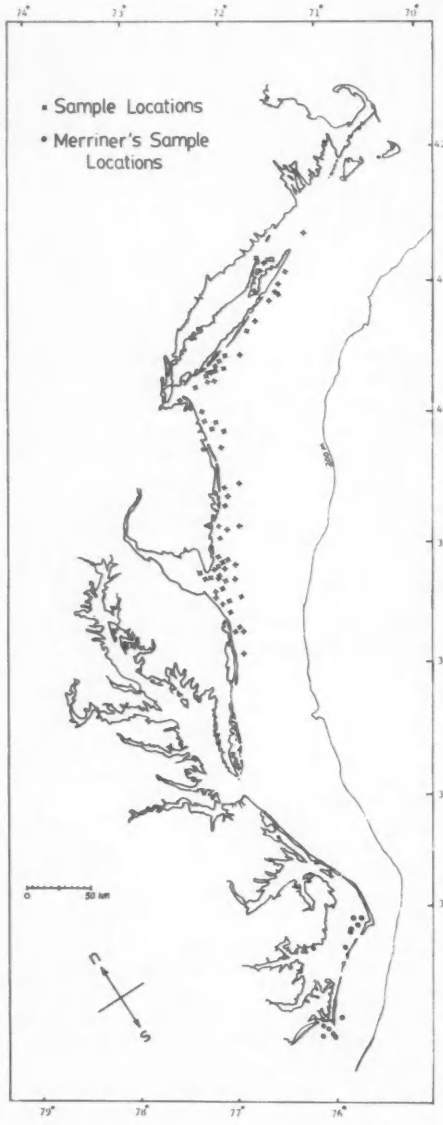

FIGURE 1.—Sampling locations for weakfish, *Cynoscion regalis*, in the New York Bight and North Carolina site of Merriner (1976).

Maturity and Fecundity Methods

The maturity stage of each sample was categorized as immature, developing, ripe (spawning), spent, or recovering as modified from Nikolsky (1963). The maturity stages were further subdivided as mature or immature for calculation of length at 50% maturity using probit analysis (Finney 1971).

Seasonality of reproduction was determined from changes in the gonad condition. A gonosomatic index (GSI) was calculated to show changes in gonad weight relative to somatic weight (gutted body weight). The index was computed as

$$GSI = (\text{gonad weight}/\text{somatic weight}) \times 100.$$

To examine physiological changes associated with spawning, liver condition was assessed using a hepatosomatic index (HSI) computed by substituting liver weight for gonad weight in the above relationship (Htun-Han 1978). The differences in monthly mean HSI between sexes were analyzed statistically using a Wilcoxon test (Patzner and Adam 1981).

The number of spawnings in the season were investigated by analyzing the seasonal frequency distribution of oocyte diameters (Hickling and Rutenberg 1936). In each of 15 samples collected between 5 May and 22 July 1980-81 in Delaware and Gardiners Bays, three subsamples were taken per ovary and about 500 oocyte diameters were randomly measured using an ocular micrometer.

Fecundity estimates were determined from 28 fish macroscopically classified as developing,

which were captured during May 1981 in Delaware and Gardiners Bays. An oocyte diameter of 0.20 mm was determined from diameter frequency distributions and the degree of yolk accumulation as the size between oogonia and developing ova, and was used as the lower size limit of ova in the fecundity estimates. Each sample was diluted with distilled water, stirred, then several aliquots removed from the solution to provide a density of about 10,000 ova in a 6 × 6 cm gridded petri dish. About 800-1,000 ova were counted from six randomly selected squares, then adjusted for a total subsample count. Two subsamples were counted per sample and three if the ova sample was from a large fish (>60 cm). The sample and subsample were oven dried at 40°C for a minimum of 24 h then weighed to the nearest 0.001 g on a Mettler[3] balance. Total fecundity was calculated as

Total fecundity = [number in subsample × (sample wt/subsample wt)] + number in subsample.

Predictive equations of fecundity from length and weight were fit to a geometric mean (GM) functional regression (Ricker 1975) following log-log transformation.

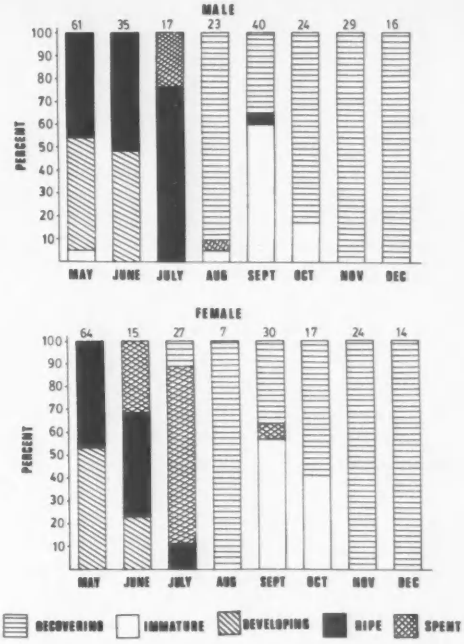

FIGURE 2.—Changes in visual maturity stage of weakfish, *Cynoscion regalis*, in 1980-81 for the New York Bight. *N* indicated for each month.

RESULTS

Seasonality

The changes in maturity stages during the year indicate spawning takes place from May to mid-July for weakfish in Delaware Bay and north to Long Island (Fig. 2). In May, all 122 mature fish examined of both sexes were in the developing or ripe stage of gonad development. The 50 fish that were inspected in June included 100% of the males and 70% of the females in a developing or ripe stage. Several of the ovaries examined in a June sample from Gardiners Bay had the appearance of being partially spent. The ovary was flaccid, slightly hemorrhaged and the lumen filled with fluid, but a few transparent ova were still visible. Spawning weakfish in Delaware Bay were captured as late as 12 July, when 11% of the females and 76% of the males were classified as ripe. In the same month, 84% of the females were in spent condition. By August, all of the fish examined at all locations were in postspawning condition. Weakfish from Sandy Hook Bay were not available until June and all the samples examined from this area were in postspawning condition, either spent or recovering.

This seasonality of spawning at each of the sample locations was suggested by seasonal changes in the GSI. Mean GSI values (percent gonad weight relative to somatic weight) ± 95% C.I. (Confidence Interval) of all females rose from 5.75 ± 1.29 in May to a peak value of 6.04 ± 1.43 in June, then declined to 1.76 ± 0.40 by July (Fig. 3). Male GSI were at a yearly high of 4.88 ± 1.45 in May but declined to only 2.51 ± 0.85 by July. The mean GSI values for females were consistently higher in all months except July. Gonad size reached the lowest levels for both sexes in August with mean GSI values of 0.71 ± 0.07 and 0.19 ± 0.02 for females and males, respectively. The GSI values remained low until the last samples were collected in November.

Specific spawning time, as reflected in GSI, was dependent on the size of the individual fish (Fig. 4).

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

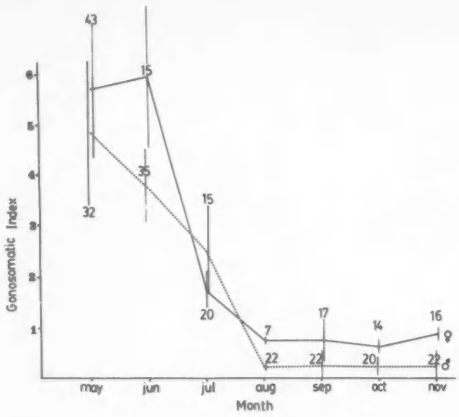

FIGURE 3.—Mean monthly gonosomatic indices ±95% C.I. of weakfish, *Cynoscion regalis*, for 1980 in the New York Bight. *N* values at each point.

Mean index values and lengths ±95% C.I. for developing fish in Delaware and Gardiners Bays during May was 2.48 ± 0.67 at a mean length of 551 ± 47.0 mm for females and 1.13 ± 0.85 at a length of 391 ± 98.9 mm for males. Spawning fish captured during May had GSI of 8.65 ± 1.64 at mean length of 702 ± 25.2 mm for females and 6.49 ± 1.58 at mean length of 619 ± 33.1 mm for males. In June, spawning fish had mean GSI values of 6.72 ± 1.83 with mean length of 544 ± 95.6 mm for females and 4.54 ± 1.04 with mean length of 570 ± 56.3 mm for males. These index variations confirmed observations of earlier spawning by large fish.

Seasonal variation in mean HSI of Delaware and Sandy Hook Bay samples indicates that changes in liver weight occurred at the time of spawning and prior to fall migration (Fig. 5). Mean HSI values ±95% C.I. for females decreased from a high in May of 2.80 ± 0.35 to a low in September of 0.87 ± 0.30. The index values for males followed the same pattern declining from 1.89 ± 0.27 in May to 0.96 ± 0.18 in September, but the maximum values occurred in November with a mean HSI of 2.57 ± 0.29. The indices were tested for differences between sexes and the differences were found to be significant in May and June ($P < 0.001$) with the values for females being greater (Table 1). No significant differences were found in a comparison of the July through November samples.

Frequency distributions of oocyte diameters from 15 fish, ranging from 55 to 81 cm and collected between 6 May and 22 July show one seasonally progressing mode of developing ova (Fig. 6). The position of the mode varied according to the development stage of the individual ovary. A sample from 5 May had a mode between 0.02 and 0.45 mm and was skewed toward a prominent peak at 0.12 mm. In the 13 May sample, a second mode appeared around 0.35 mm and this mode increased to a size of 0.63 mm in the 20 June sample. The 22 July sample contained only oogonia. Maximum ova diameter observed was 0.95 mm from a sample on 26 May. That ovum was filled with fluid between the yolk and chorion, indicative of an ova immediately prior to release (Bagenal 1967). This corresponds to the size of weakfish eggs, 0.870-0.975 mm, which have been identified in the water column (Harmic 1958).

TABLE 1.—Wilcoxon (Mann-Whitney) test comparing hepatosomatic indices between sexes of weakfish, *Cynoscion regalis*, from the New York Bight for June through November 1980 and May 1981. S = Wilcoxon test statistic, Z = critical value.

	S	*N*	Z	Probability level
1980				
June	622.0	50	5.081	0.0001***
July	194.0	34	−1.767	0.0865
August	106.0	28	0.265	0.7928
September	274.0	37	−0.904	0.3658
October	252.0	35	0.017	0.9867
November	283.5	40	−1.215	0.2318
1981				
May	332.0	48	−3.782	0.004***

*** = highly significant differences.

Maturity, Sex Ratio, and Fecundity

Length ±95% C.I. at which 50% of the total sampled population reached maturity was similar for both sexes. Females attained 50% maturity at 25.6 ± 1.2 cm, while males were slightly lower at 25.1 ± 1.1 cm (Table 2). The corresponding age at maturity for both sexes was 1 yr. The smallest mature male and female was 20 cm. The maximum size of immature weakfish was 40 cm for females and 33 cm for males.

The overall population sex ratio approached equality (Table 3). The sex ratio of the population, divided into 5 cm length intervals, was 48:52 females to males and was not significantly different from 50:50 as determined from a chi-square analysis ($\chi^2 = 1.81$, $\chi^2_{0.05} = 3.84$, $n = 1{,}669$). Sex ratio at size data did reveal significant differences from 50:50 for several length intervals. At 40 cm, the ratio was 52:48 female to male but increased to

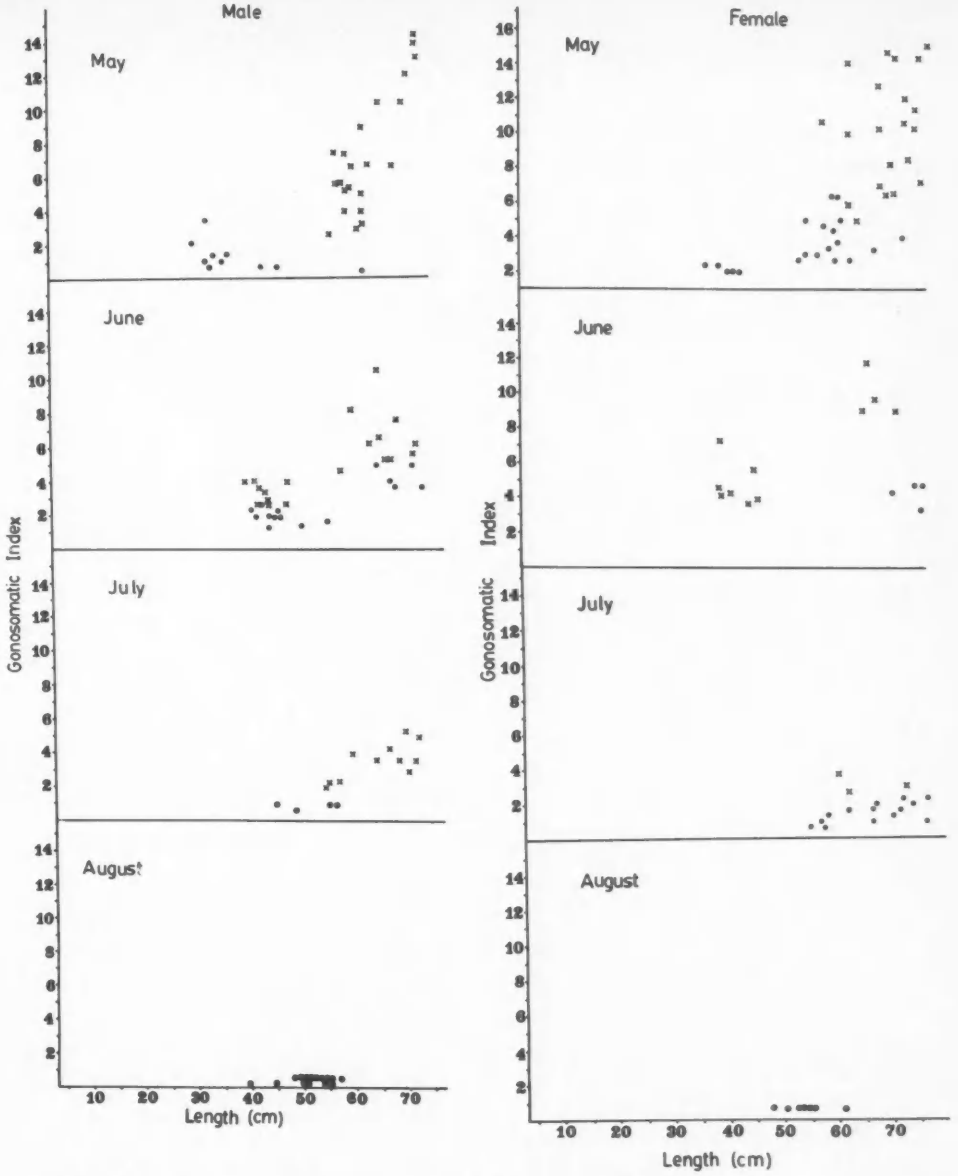

FIGURE 4.—Monthly gonosomatic indices of individual weakfish, *Cynoscion regalis*, by sex for 1980. Spawning fish indicated by x.

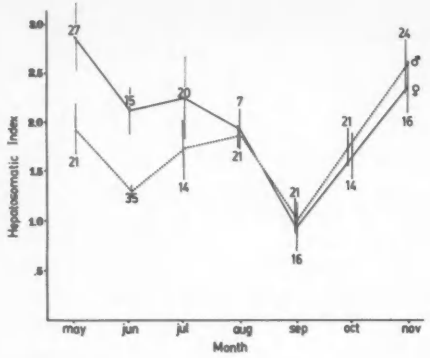

FIGURE 5.—Mean monthly hepatosomatic indices ±95% C.I. of weakfish, *Cynoscion regalis*, for 1980 with *N* indicated at each point.

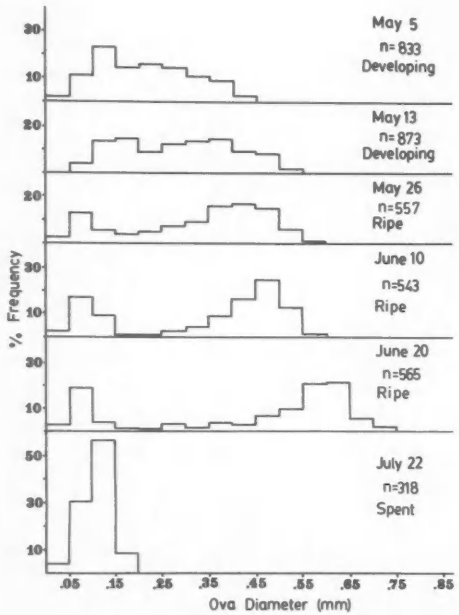

FIGURE 6.—Monthly frequency of oocyte diameters for weakfish, *Cynoscion regalis*, in the New York Bight for 1980-81.

60.5% ($\chi^2 = 5.25$, $\chi^2_{0.05} = 3.84$, $n = 119$) and 63.8% ($\chi^2 = 7.19$, $\chi^2_{0.01} = 6.64$, $n = 94$) males at 45 and 55 cm, respectively. The sex ratio of combined length intervals above 55 cm had a ratio of 58.5:41.5

TABLE 2.—Length at maturity for weakfish, *Cynoscion regalis*, from 1980 to 1983.

Length (cm)	Female		Male	
	N	% mature	*N*	% mature
18	15	0.0	16	0.0
19	7	0.0	11	0.0
20	8	12.5	11	9.1
21	11	18.2	5	40.0
22	8	37.5	9	33.3
23	13	53.8	16	31.3
24	11	45.5	12	50.0
25	13	46.2	12	75.0
26	14	71.4	15	86.7
27	17	88.2	14	71.4
28	10	80.0	20	65.0
29	17	82.4	22	63.6
30	19	100.0	17	82.4
31	18	88.9	14	85.7
32	16	93.8	20	85.0
33	10	90.0	17	94.1
34	14	85.7	15	100.0
35	7	85.7	3	100.0
36	10	80.0	8	100.0
37	9	77.8	12	100.0
38	15	100.0		
39	14	85.7		
40	13	92.3		
41	4	100.0		
42	10	100.0		
43	10	100.0		
Total	313		269	
Size at 50% mature	25.6		25.1	
95% Confidence Interval	24.4-26.8		24.0-26.2	

TABLE 3.—Sex ratios (female:male) of weakfish, *Cynoscion regalis*, in the New York Bight.

Length[1]	Ratio	χ^2
15	27:40	2.52
20	72:73	0.01
25	149:174	1.93
30	148:157	0.27
35	72:73	0.01
40	71:65	0.26
45	42:72	5.25*
50	35:40	0.33
55	34:60	7.19**
60	36:35	0.01
65	35:27	2.00
70	31:28	0.15
75	28:17	2.69
80	18:1	15.21***
85	4:0	4.0*
Total	807:862	1.81

[1]Midpoint of length interval (12.5 to 17.5, etc.).
* = significant difference $P < 0.05$.
** = significant difference $P < 0.01$.
*** = significant difference $P < 0.001$.

which was significantly dominated by females ($\chi^2 = 7.45$, $\chi^2_{0.01} = 6.64$, $n = 260$).

Regression models indicated that length and weight were equally predictive of fecundity. The relationships between total length or gutted weight, and fecundity were best described by a power curve. The GM functional regression (Ricker 1975) of the $\log_e$ transformed data ± standard error of the regression were

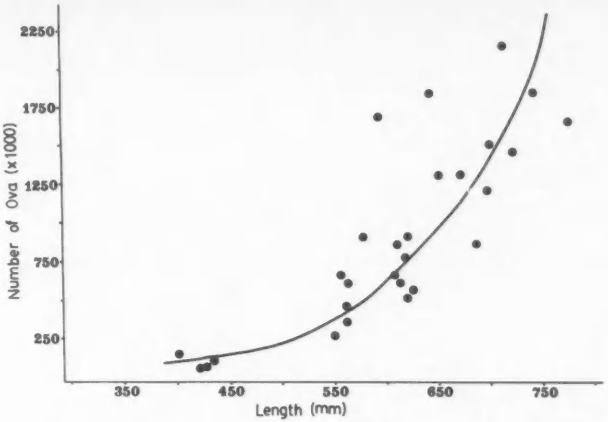

FIGURE 7.—Fecundity as a function of length for weakfish, *Cynoscion regalis*, in New York Bight for 1981.

$$\ln \text{fecundity} = -16.322 + 4.659 \ln \text{total length (mm)} \pm 0.368$$
$$r^2 = 0.835 \quad n = 28 \quad \text{Figure 7}$$
$$\ln \text{fecundity} = 1.975 + 1.542 \ln \text{gutted weight (g)} \pm 0.364$$
$$r^2 = 0.839 \quad n = 28.$$

Fecundities were also estimated for six weakfish collected in June from Gardiners Bay which appeared to be spent, although they had ova remaining in the gonad. These ova were 0.55 to 0.65 mm which were similar in size to those present in a ripe ovary. All six samples were significantly different ($P < 0.001$) than expected values based on a Students *t*-test (Table 4). These June samples were 60-75% lower than the predicted fecundities at length.

TABLE 4.—Difference between expected fecundity (based on ln fec = −16.322 + 4.659 ln TL) and observed fecundity for 6 weakfish, *Cynoscion regalis*, collected 27 June 1981, in Gardiners Bay, N.Y.

Total length (mm)	Fecundity estimate		% Difference
	Expected	Observed	
590	650,171	196,891	69.7
613	777,718	93,579	88.0
615	789,675	105,919	86.6
704	1,487,262	438,909	70.5
737	1,843,210	650,600	64.7
644	979,893	313,054	68.1
			$\bar{x}$ = 74.6

DISCUSSION

Weakfish spawning in northern estuaries is a seasonal event which occurs following the spring inshore migration. (Welsh and Breder 1923; Hildebrand and Schroeder 1928). Our study found the spawning period for weakfish in Delaware Bay and Gardiners Bay, as determined from maturity stages, to be from May to mid-July. Ichthyoplankton surveys have found weakfish eggs and larvae present in New York Bight from May to July (Colton et al. 1979). The spawning period was further substantiated by changes in GSI. The mean GSI values reached a maximum in May for males and in June for females, then both declined to minimum values by August. The gonad weights were maintained at this low level until the fish disappeared from the coast in late November. The spawning period of weakfish in North Carolina is somewhat longer, extending from March to September with the peak period from April to June (Merriner 1976). The duration of the ripe maturity stage in Delaware and Gardiners Bays was greater for males, with ripe males captured as late as 22 July. The protracted spawning season of males was also evident in the GSI values. July was the only month in which male indices were greater than those of females, indicating that the gonad weight per unit body weight was larger in males. In other months, female GSI values were as much as 2.8% greater than males.

Sex differences were also evident in physiological changes associated with spawning. HSI values were near maximum in May, during spawning season, and as expected higher in females. Devel-

opment of ovaries demands higher energetic costs than testicular development (Nikolsky 1963); therefore, the necessary energy reserves in the liver would be proportionately larger in females (Timashova 1982). After spawning, the sexual dimorphism disappears and HSI values for both sexes increase similarly prior to the fall migration.

The peak spawning period in the New York Bight estuaries varied with different size weakfish. Generally, among migratory fishes, the larger individuals will return to an estuary prior to their smaller counterparts (Briggs 1955; Nikolsky 1963). Weakfish exhibit a similar behavior, as the largest individuals or "tiderunners" enter the bays in early May and spawn by mid-May, whereas the smaller weakfish arrive later and reach peak spawning during June. The GSI values for fish >60 cm generally decline from May to June, while smaller fish increase to maximum values in June. This differential spawning based on parental size results in two spawning peaks and the subsequent appearance of bimodal length-frequency data for juvenile weakfish (Daiber 1954; Thomas 1971; Shepherd and Grimes 1983).

Sex Ratio, Maturity, and Fecundity

The overall sex ratio of the population is not different from 1:1, but one sex was dominant at certain length intervals. We believe the deviations from a 1:1 ratio at various lengths were attributable to differential growth between sexes (Wenner 1972). Female growth begins to exceed male growth at about 45-55 cm (Shepherd and Grimes 1983), at which point the sex ratio becomes dominated by males. Females grew beyond that size interval faster and occupied the majority of the 60-85 cm length intervals. Although males have growth potential equal to females, the numbers attaining maximum size were greater for females.

In northern waters, the size at which weakfish attained 50% population maturity was similar for both sexes. Females matured by 25.6 cm at age 1 while males attained maturity at 25.1 cm, also at age 1. Apparently, greater differences exist between northern weakfish (Delaware Bay and north) and southern weakfish (North Carolina). Although ages were similar, southern females spawned at 23 cm and males by 18 cm (Merriner 1973).

Estimates of fecundity for New York Bight weakfish differ from estimates for southern weakfish. Weakfish in North Carolina did not reach sizes much beyond 45 cm but had fecundities, relative to length, several times higher than northern weakfish (Merriner 1976) (Table 5). For example, at 50 cm TL female weakfish from New York Bight produced 306,159 ova, while the fecundity of southern fish of the same size was 2,051,080 ova. In spite of these large differences, lifetime fecundity would be approximately equal. Southern weakfish can potentially reproduce until age 5 and produce about 9,913,080 ova (based on the equation, fecundity = $0.152\ TL^{2.6418}$, from Merriner 1976), whereas northern weakfish reproducing for 10 yr have nearly equivalent total ova production of 10,008,167.

Batch spawning, involving two distinct groups of ova, was found for weakfish in North Carolina (Merriner 1976). In samples examined in 1980-81 from Delaware and Gardiners Bays, multiple spawns were not evident. The ova diameter frequencies of developing and ripe ovaries contained two modes, one consisting of reserve oocytes and another of developing ova. The developing ova had a wide size range (≈0.3 mm) and may have been released during consecutive spawning events, but did not constitute separate batches within an ovary. Furthermore, all ova produced annually by weakfish may not be released during spawning. A study of Delaware Bay weakfish in 1954 proposed batch spawning, but spent ovaries were not examined to determine if all ova were released (Daiber 1954). Ovaries classified as spent which we examined still contained 25-40% of the ova expected for a fish of that size. These results suggest fertility may be 60-75% of estimated potential fecundity. Foucher and Beamish (1980) reported similar conclusions from studies of Pacific hake, *Merluccius productus*. We did not examine

TABLE 5.—Comparison of fecundity for weakfish, *Cynoscion regalis*, between Cape Hatteras (Merriner 1976) and New York Bight.

	Fecundity comparisons			
	Cape Hatteras		New York Bight	
Age	SL	Fecundity	TL	Fecundity
0	159	149,429		
1	225	391,688	203	4,593
2	286	762,258	323	39,978
3	357	1,410,550	479	250,685
4	421	2,229,220	578	601,544
5	562	4,969,940	638	953,027
6			677	1,256,487
7			701	1,477,902
8			728	1,762,445
9			758	2,127,278
10			763	2,193,448
Cumulative fecundity		9,913,085		10,667,387

enough spent weakfish ovaries to determine if this phenomenon was consistent from year to year.

The variable reproductive and age and growth characteristics for weakfish in different geographic areas suggest specific physiological responses to different environmental conditions. North Carolina weakfish had smaller sizes at maturity, smaller length at corresponding age after age 1, reduced longevity and maximum size, and higher relative fecundity than New York Bight weakfish. However, the lifetime reproductive potential was nearly equal for both groups. These life history characteristics for weakfish are similar to clinal variations between Labrador and Florida described for American shad (Leggett and Carscadden 1978), differences in reproductive characteristics between Atlantic herring, *Clupea harengus harengus*, in the Norway and the Baltic Sea (Schopka 1971), and north to south variations in North American populations of Pacific herring, *Clupea harengus pallasi* (Paulson and Smith 1977).

The different reproductive strategies in weakfish may result from varying environmental demands. When weakfish spawning occurs in northern estuaries, water temperatures are unpredictable and subject to sudden drops which are potentially lethal to eggs and larvae (Harmic 1958). Table 6 shows minimum estuarine temperatures during the spawning season in northern waters may drop below the temperature limits of 12°-16°C necessary for successful hatching (Harmic 1958). The higher probability of prereproductive mortality of progeny in northern estuaries results in a "bet-hedging" strategy in which fewer eggs are produced each year, but the possible number of annual spawnings are increased (Stearns 1976; Giesel 1976), thus maximizing potential contributions to the gene pool throughout a fish's lifespan. In contrast, southern weakfish spawn in a more predictable estuarine environment (Table 4) and, consequently, there is less chance of environmentally induced prereproductive mortality. However, southern fish are faced with greater postreproductive mortality (longevity observed by Merriner (1973) was 5 yr). Greatest reproductive success in this situation requires maximizing annual gamete production in the few years possible. In addition, weakfish migrating to northern estuaries (Nesbit 1954) may utilize energy reserves otherwise available for gonad growth, whereas southern fish having less distance to travel may reallocate energy towards reproduction.

TABLE 6.—Surface water temperatures (°C) for April-July in Plum Island, N.Y.; Cape May, N.J.; Gloucester Point, Va; and Beaufort, N.C.[1]

	April	May	June	July
Plum Island, N.Y.				
$\bar{x}$	5.6	9.7	14.6	18.8
Max	9.0	18.0	20.0	24.0
Min	2.0	4.0	9.0	15.0
$\bar{x}$max	7.7	13.4	17.7	21.4
$\bar{x}$min	3.3	6.4	11.4	16.3
Cape May, N.J.				
$\bar{x}$	10.2	14.5	20.0	22.6
Max	17.0	21.0	25.0	28.0
Min	6.0	9.0	12.0	18.0
$\bar{x}$max	14.6	18.9	23.8	25.6
$\bar{x}$min	7.0	10.8	15.7	19.9
Gloucester Point, Va.				
$\bar{x}$	13.1	19.1	23.8	26.5
Max	21.0	26.0	30.0	32.0
Min	7.0	13.0	17.0	21.0
$\bar{x}$max	17.1	22.4	27.0	29.0
$\bar{x}$min	9.6	15.6	20.4	24.1
Beaufort, N.C.				
$\bar{x}$	17.2	21.4	25.2	27.4
Max	21.0	26.0	32.0	30.0
Min	14.0	14.0	18.0	24.0
$\bar{x}$max	20.3	24.2	28.3	29.2
$\bar{x}$min	14.3	17.5	21.9	25.8

[1]National Ocean Survey. 1972. Surface water temperature and density; Atlantic coast, North and South America. 4th ed. NOS Publ. 31-1, p. 1-109.

Consequences of the area specific reproductive characteristics may be a reduced population stability for weakfish in the northern end of the range. Apparently, northern fish have a strategy to cope with potentially higher egg and larval mortality by spreading reproduction over more years and reducing annual fecundity, i.e., a "bet-hedging" strategy (Stearns 1976). Therefore, to fulfill their reproductive potential they must avoid premature adult mortality. If adult mortality (natural and fishing) in weakfish becomes excessive, the larger, most fecund individuals will be lost or reduced, thus shifting the burden of spawning to the smaller, less fecund fish. When the value of b in the fecundity equation $F = a\mathrm{TL}^b$ is >3, as in New York Bight weakfish, then truncation of the size/age structure in a spawning population will also result in a reduction of population fecundity (Hempel 1979). Concurrent high adult mortality and high prereproductive mortality could contribute to a decline in population abundance. The large fluctuations which have occurred in weakfish populations over the last several decades (Wilk 1979) may be due in part to these circumstances (i.e., high adult and prereproductive mortality). Although the correlation between population fecundities and recruitment is not usually strong for marine fishes (Cushing 1977), a decrease in population fecundity may eventually

reduce any buffer that weakfish have of withstanding natural fluctuations in egg, larval, and juvenile survival. Therefore, if management practices are to effectively regulate the weakfish resources, geographic variations in reproductive potential should be considered.

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FIELD AND LABORATORY OBSERVATIONS ON DIURNAL SWIM BLADDER INFLATION-DEFLATION IN LARVAE OF GULF MENHADEN, *BREVOORTIA PATRONUS*

D. E. HOSS[1] AND G. PHONLOR[2]

ABSTRACT

Diurnal swim bladder inflation-deflation in gulf menhaden larvae was studied at sea and in the laboratory. At sea, the larvae filled their swim bladders at night and deflated them during the day. Laboratory experiments in which the larvae were either prevented or allowed to reach the air-water interface demonstrated that the larvae fill their swim bladder each night by swallowing air. These results agree with the findings of other investigators and suggest that diurnal swim bladder inflation may be a common characteristic in the late stage larvae of clupeoid species.

The swim bladder in fishes has been assigned various functions, the most widespread being the regulation of buoyancy. Recent work on clupeoid species, however, has shown that the function of the swim bladder changes with ontogeny. In adults of at least two clupeoids—Atlantic herring, *Clupea harengus*, and Atlantic menhaden, *Brevoortia tyrannus*—the swim bladder is thought to serve as a reserve of gas for the adjustment of hydrostatic pressure in the gas-filled bulla, allowing the bulla membrane to maintain acoustic sensitivity independently of depth. The swim bladder's role as a buoyancy regulating organ is secondary (Blaxter and Hunter 1982). During the late larval stages of some clupeoids, however, buoyancy provided by an inflated swim bladder may have an important function. Hunter and Sanchez (1976), working with the pelagic larvae of the northern anchovy, *Engraulis mordax*, proposed that an observed diurnal inflation and deflation of the swim bladder by larvae is an energy-sparing mechanism. In this case, one function of the inflated swim bladder is to provide buoyancy that allows the larvae to "rest" during the night when they are unable to see to feed. This diurnal inflation and deflation of the swim bladder has also been reported for other larval clupeoids by Uotani (1973).

The objective of this study was to determine if a diurnal swim bladder inflation-deflation rhythm exists in larval gulf menhaden, *Brevoortia patronus*, under natural conditions and, if so, to evaluate the mechanism of inflation in the laboratory.

The swim bladder in gulf menhaden is similar to that described for Atlantic menhaden by Hoss and Blaxter (1981). In the Atlantic species the anlage of the swim bladder is present at 10 mm standard length (SL), and the pro-otic bullae first appear at 12.5 mm and may contain gas soon after. The swim bladder first contains bubbles of gas in 13 mm SL larvae, and the lateral line first appears in larvae of about 17 mm. In the fully developed system, narrow ducts connect the swim bladder to the gas-filled bullae which are close to the labyrinth of the inner ear. The bullae-swim bladder system is in turn connected to the extensive lateral line on the head of adult fish through a membrane in the skull. As in other clupeoid species (Blaxter and Hunter 1982), menhaden apparently swallow air to initially fill both the bullae and the swim bladder. As there is no evidence for gas secretion in menhaden, it is also assumed that they replace lost gas by regularly swallowing air into the alimentary canal and then by transferring it to the swim bladder through the pneumatic duct. The swim bladder is deflated by diffusion and by reversing gas movement in the above pathway. Unlike some clupeoids, menhaden have no direct connection between the swim bladder and the anal opening (Tracy 1920).

METHODS

At Sea

Gulf menhaden larvae were obtained in the northern Gulf of Mexico off Southwest Pass, La.,

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at the mouth of the Mississippi River in December 1981 (RV *Oregon II* cruise 123) and December 1982 (RV *Oregon II* cruise 131). On cruise 123, larvae were collected by oblique or surface tows of either a multiple-opening closing net and environmental sensing system (MOCNESS) (Wiebe et al. 1976), a neuston net, or an opening-closing paired BFN-1 net[3]. The sampling scheme was modified on cruise 131 in that only the MOCNESS system was used and duplicate samples were taken at fixed depths (1, 8, and 20 m) during a 24-h period of time. On board the ship, menhaden larvae were removed from the samples, measured to the nearest 0.1 mm SL, and examined for the presence of gas in the swim bladder. Gas in the swim bladder was easily observed before pigmentation of larvae (Fig. 1). In inflated bladders, a light-refractive bubble is obvious while a deflated bladder appears under the microscope as a flattened sac (Doroshev et al. 1981). Maximum width and length of the swim bladder (with or without gas) was measured to the nearest 0.02 mm, and volume was calculated by the equation for a prolate spheroid, $V = 4/3\ \pi\ ab^2$, where a is half the maximum bladder length and b is half the maximum bladder width (Hunter and Sanchez 1976). Approximate changes in volume of the swim bladder due to increased pressure at increased depth of capture were calculated from Boyle's law $\frac{P_1}{P_2} = \frac{V_2}{V_1}$ where P is pressure and V is volume, and temperature is assumed to be constant. After being measured, larvae were preserved in 5% Formalin[4].

In the Laboratory

Experiments to determine if larvae filled the swim bladder by gulping in air at the water surface utilized larvae hatched from eggs in the laboratory (Hettler 1983). Larvae were reared on the rotifer *Brachionus plicatilis*, also cultured in the laboratory. As larvae grew older, their diet was supplemented with newly hatched *Artemia* nauplii. Before being used, larvae were held in 80 l tanks at a water temperature of 20°C, salinity of ca. 25‰, and a 12 h light-12 h dark photoperiod without a dawn or dusk transition.

Three hours before the start of the experiment, 15-20 larvae were transferred from the rearing tanks to each of eight 10 l tanks, and 10 larvae were measured and observed for the presence of gas in the swim bladder. A 500 μm screen was then placed below the water surface (Fig. 2) in four of the experimental tanks to prevent access of the larvae to the air-water interface. In the other four tanks, larvae had access to the air-water interface. During the experiment, the 12-h-light photoperiod was continued. Larvae sampled at ca. 1800, 2100, 0630, 0900, and 1230 h were measured and observed for gas in the swim bladder.

[3]Tarez and Co., 8460 S.W. Street, Miami, FL 33143.

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

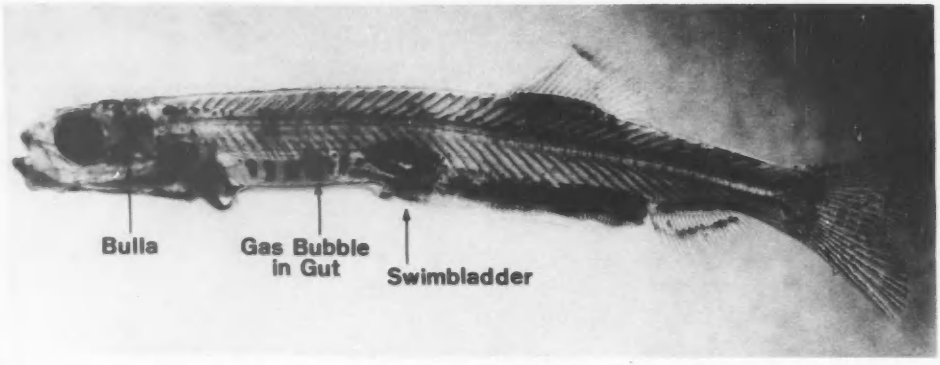

FIGURE 1.—Larval gulf menhaden, *Brevoortia patronus*. Inflated swim bladder, gas-filled bullae, and gas bubble in foregut are indicated by arrows.

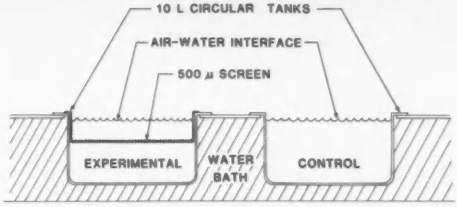

FIGURE 2.—Cross section view of tanks used in laboratory experiments to determine if larvae of gulf menhaden, *Brevoortia patronus*, fill the swim bladder at the water surface.

RESULTS

At Sea

The percentage of larvae having gas in the swim bladder was much greater at night than during the day (Fig. 3). The number of larvae with gas increased within an hour of sunset and decreased within an hour of sunrise (i.e., within the twilight periods). Although sample size was sometimes small (8-10 fish), the combined data for the two cruises were consistent.

The volume of gas in the swim bladder of larvae captured at night was greater than the volume of gas in larvae captured during the day (Table 1). There was a significant difference between the day and night volumes, where sample size was sufficient to allow testing. Sunrise and sunset samples were not significantly different (t-test, $P > 0.05$) from daylight samples.

Gulf menhaden larvae showed a diurnal pattern of depth distribution that seemed to contrast the pattern of swim bladder inflation (Table 2). Night sampling (1700-0600) indicated that larvae were present from the surface down to at least 20 m, the deepest samples taken. Maximum water depth at

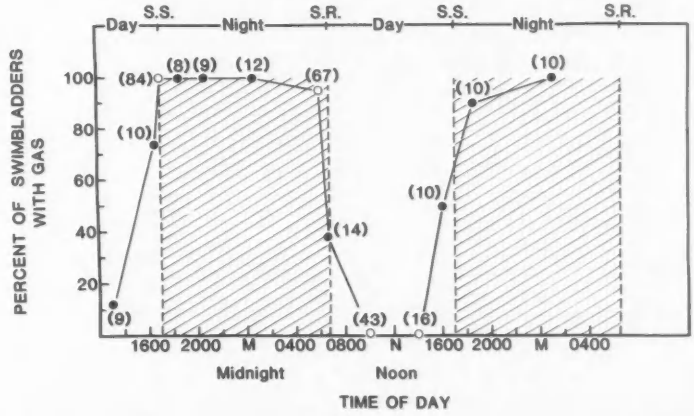

FIGURE 3.—Diurnal change in percent of gulf menhaden, *Brevoortia patronus*, larvae with gas in their swim bladders (S.S. = sunset, S.R. = sunrise). Numbers of fish examined are in parentheses. Data from two cruises (Dec. 1981, open circles; Dec. 1982, closed circles) are combined and presented in chronological order.

TABLE 1.—Swim bladder volume of gulf menhaden, *Brevoortia patronus*, larvae measured immediately after capture. Samples are from oblique and surface net tows.

Length class (mm)	Night samples N	Night samples Swim bladder vol. (mm³) (mean ± 2 SE)[1]	Day samples N	Day samples Swim bladder vol. (mean ± 2 SE)[1]	t	df	P
<14.9	7	0.44 ± 0.19	1	0.03	—	—	—
15-16.9	13	0.89 ± 0.21	9	0.05 ± 0.02	7.97	20	<0.001
17-18.9	18	1.71 ± 0.52	12	0.17 ± 0.10	5.81	28	<0.001
>19.0	11	1.78 ± 0.75	8	0.32 ± 0.19	3.77	17	<0.01

[1]SE = standard error of the mean.

TABLE 2.—Swim bladder volume of gulf menhaden, *Brevoortia patronus*, larvae captured in MOCNESS tows and measured immediately after capture. Volumes were corrected for expansion of the swim bladder due to the change in pressure (0.1 atm/m of water).

Water depth (m)	Night samples N	Night samples Swim bladder vol. (mm³) (mean ± 2 SE)[1] At surface	Night samples Corrected for pressure change	Night samples % with gas	Day samples N	Day samples Swim bladder vol. (mean ± 2 SE)[1] At surface	Day samples Corrected for pressure change	Day samples % gas
1	55	0.422 ± 0.148	NA	97	54	0.033 ± 0.013	NA	0
8	75	0.593 ± 0.136	0.329 ± 0.075	99	3	([2])	—	0
20	21	0.336 ± 0.123	0.126 ± 0.044	97	0	—	—	—

[1]SE = standard error of the mean.
[2]Swimbladder volume of the three fish captured was not measured.

this station varied between 23 and 27 m. During the day nearly all the larvae were taken at the surface and only three larvae were captured as deep as 8 m. Without exception, fish examined from daylight samples did not have gas in the swim bladder, while almost all of the fish from the night samples contained some gas. In some cases, the volume of the swim bladder was such that it constricted the gut (Hunter and Sanchez 1976) or burst through the body wall.

The volume of gas in the larval swim bladder would, of course, be reduced due to increased pressure as the larvae moved deeper in the water. As the volume of the swim bladder decreased, its capacity as a buoyancy organ would decrease, causing the larvae to expend more energy in swimming or to sink more rapidly. Since our measurements were all made at the surface, we corrected the volumes of the swim bladders in larvae collected at 8 and 20 m to reflect the increased pressure at these depths (Table 2). Since swim bladder volume is related to size of the fish, a t-test was used to compare the mean standard length of the larvae from each depth. This test showed no significant difference in lengths of fish captured at the three depths (t-test, $P > 0.05$).

In the Laboratory

Swim bladder volume was much greater in tanks where the larvae had direct access to air (Fig. 4). Swim bladder volume of the larvae without access to air remained essentially the same throughout the experiment. It appears from this experiment that gulf menhaden larvae, like a number of other clupeoid species, fill their swim bladders by swallowing air at the surface.

DISCUSSION

Our findings for swim bladder inflation in larval gulf menhaden generally agree with the findings of Hunter and Sanchez (1976) and Uotani (1973) for other clupeoid species. Our field studies showed conclusively that gulf menhaden inflate their swim bladders at night and deflate them during the day. Hunter and Sanchez (1976) suggested that nighttime swim bladder inflation in larvae of the northern anchovy is an energy-sparing mechanism that allows larvae to reduce swimming activity during nonfeeding periods while maintaining their depth in the water column. These authors further suggest that a reduction in swimming activity may reduce predation, since some predators of larval fish (e.g., chaetognaths) use the water movement caused by swimming activity to detect their prey.

In the laboratory we found that larvae were unable to fill their swim bladders when they were prevented from reaching the air-water interface. This too agrees with the previous hypothesis on

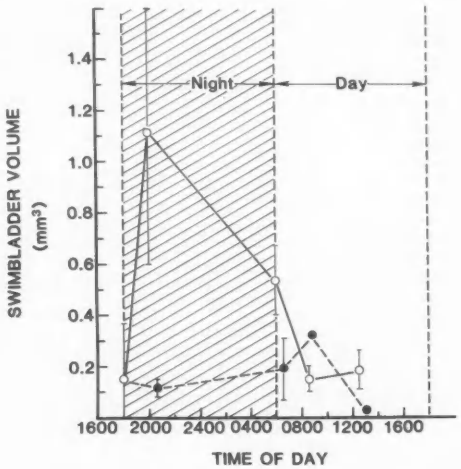

FIGURE 4.—Swim bladder volume ($X \pm 2$ SE) of gulf menhaden, *Brevoortia patronus*, held in the laboratory with access (solid line) and without access (dashed line) to the air-water interface.

how larvae of physostomatous clupeoid fishes initially inflate the swim bladder (Blaxter and Denton 1976).

Under field conditions, gulf menhaden larvae began to fill and empty their swim bladders during the approximately 45 min of twilight preceding sunset and sunrise. The numbers of fish with gas in their bladders increased and decreased gradually (i.e., it is not an all or none phenomenon) prior to darkness (or daylight). This observation suggests to us that larvae are responding as individuals to gradually changing light levels. This response is probably better developed in larger larvae.

The relation of diurnal vertical migration to swim bladder inflation that we found is different from the generally accepted position that larvae are near the sea surface with well-inflated swim bladders at night and are deeper in the water with deflated swim bladders during the day. We captured menhaden larvae at three discrete depths at night (down to 20 m) and over 95% of the larvae captured at 8 and 20 m had gas in their swim bladders. On four previous cruises, collections in the same location also showed that menhaden larvae were distributed throughout the water column at night but concentrated at the surface during the day (unpubl. data[5]).

In conclusion, the swim bladder of the larval stages of gulf menhaden acts as a buoyancy regulator that allows the fish to maintain a position in the water column at night without movement. By day the swim bladder is deflated, and the larvae must actively swim to maintain their position near the water surface. At some point during development, the swim bladder's primary function switches to that of a pressure-adjusting mechanism for the otic bullae.

[5]Sogard, Susan M., Donald E. Hoss, and John J. Govoni. In prep. Density and depth distribution of larval fishes at selected sites in the northern Gulf of Mexico. Southeast Fish. Cent. Beaufort Lab., Natl. Mar. Fish. Serv., NOAA, Beaufort, NC 28516-9722.

ACKNOWLEDGMENTS

Robin Berry and Susan Sogard assisted in the data analyses and laboratory work. John Govoni, William Hettler, and Susan Sogard provided critical review of the manuscript, and W. Hettler provided laboratory-reared gulf menhaden. MOCNESS sampling was conducted by Shailer Cummings (Atlantic Oceanographic and Meteorological Laboratories, NOAA) with able assistance from the crew of the RV *Oregon II*. This research was supported in part by a fellowship to the Junior author from the Brazilian National Science Council.

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NOTES

COMPARISON OF AMERICAN EEL GROWTH RATES FROM TAG RETURNS AND LENGTH-AGE ANALYSES

Estimates of growth rates of American eel, *Anguilla rostrata*, have been largely indirect, based on projections from length-age regressions or comparisons of mean lengths at particular ages (Smith and Saunders 1955; Boëtius and Boëtius 1967; Ogden 1970; Bieder 1971; Gray and Andrews 1971; Hurley 1972; Harrell and Loyacano 1980; Kolenosky and Hendry 1982). Although valid for many fish species, these two approaches may be questionable in eel studies because of high variability in lengths at given ages and because of considerable overlap in lengths among ages (e.g., Bertin 1956; Fahay 1978; Facey and LaBar 1981; Moriarty 1983). Testing the accuracy of a length-age regression as an estimator of growth rate requires a simultaneous mark-recapture study. Our objective was to mark and recapture eels in a Georgia estuary and to compare growth data from recaptures with growth estimates derived from length-age regressions and mean-length-at-age calculations for eels from the same population captured at the same time. We also sought information on seasonal growth patterns and differences in growth rates among size classes.

Materials and Methods

All American eels were captured in tidal Fridaycap Creek (lat. 31°21′N, long. 81°24′W) which enters the South Altamaha River, Ga., about 11 km from the river mouth (see Helfman et al. 1983). Salinities and water temperatures ranged from 0 to 22‰ and 5.5° to 31°C, respectively. Baited eel traps were set at or before sunset and pulled shortly after sunrise the next day. Animals were anesthetized in an ice slurry or in tricaine methanesulfonate, measured (total length), weighed, tagged with 25 mm long Floy[1] FD-68B anchor tags, and released where captured. We tagged 659 animals on eight occasions between October 1980 and December 1982. Growth data from eels at large <20 d were not used because of possible confusion with measurement error, which averaged ± 1 mm (range = 0-5 mm, $N = 35$ measurements of seven eels).

Age determinations are based on sagittal otolith analyses from 305 eels captured concurrently with tagged animals. Most otoliths had distinct opaque and transparent zones, with few apparent supernumerary zones. Seasonal analysis of otolith margins indicated that presumed annuli were deposited on an annual basis and were a reasonable chronicle of age (Helfman et al. in press). Fish used in the mark-recapture study of growth were not collected for histological examination of gonads, and we therefore could not determine if sex-related differences in growth occurred (Tesch 1977).

Results

We recaptured 101 individuals, for an overall recapture rate of 15%. Time at large ranged from 8 to 493 d. Recapture frequencies were 84 fish recaptured once, 14 recaptured twice, 2 recaptured three times, and 1 recaptured four times.

Growth rates of recaptured eels were variable but fell into two apparent seasonal categories (Table 1): 1) Slow growth from November through February (0.0-0.08 mm/d, $\bar{x} = 0.026$, SD = 0.024, $N = 13$ recaptures) and 2) fast growth during spring, summer, and fall (0.01-0.63 mm/d, $\bar{x} = 0.221$, SD = 0.152, $N = 78$ recaptures); fast period growth was significantly greater (t-test, $P < 0.001$). Combining averages, and assuming a slow period of 4 mo, yield an average annual growth

TABLE 1.—Growth rates of recaptured American eels as a function of season and year. Values in the body of the table are numbers of animals with particular growth rates. Intervals for fastest and slowest rates are subdivided by 0.05 mm/d; other intervals are 0.10 mm/d.

	Slow growth period (Nov.-Feb.)[1]	Fast growth period (Mar.-Nov.)	
Growth (mm/d)	1980-81	1981	1982
0.00-0.05	12	2	4
0.06-0.10	1	5	12
0.11-0.20		10	9
0.21-0.30		7	9
0.31-0.40		3	4
0.41-0.50			7
0.51-0.60		1	4
0.61-0.65			1
$\bar{x}$ growth (mm/d)	0.026	0.182	0.246
SD	0.024	0.107	0.172

[1]An additional 26 eels at large from late November 1982 to early May 1983, i.e., encompassing primarily the slow growth period, grew an average of 0.054 mm/d (SD = 0.034 mm/d).

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

rate of 57 mm for eels 270-500 mm long over the 2-yr studied (95% C.I. [confidence interval] = ±8.4 mm, growth periods treated as independent random variables, Bliss 1967). Growth as percent increase in length for an average eel 347 mm long was 16%.

Accuracy of the extrapolated annual estimate can be tested against independent, long-term growth data from animals whose recapture intervals included both growth periods. Seven animals had recapture intervals of 6-16 mo (Table 2); average growth was 62 mm/yr (95% C.I. = ±20.1 mm) or a 17% increase in length.

TABLE 2.—Annual growth rates of eels in Fridaycap Creek, Ga., based on long-term recaptures. Data are from eels that were at large for more than a 180-d interval that included both fast and slow growth periods.

Eel no.	Date: First capture	Date: Second capture	Days at large	Length (mm): Initial	Length (mm): Final	Growth rate (mm/yr)	Percent increase
[1]1	26-X-80	27-VIII-81	313	353	429	83	23
1	26-II-81	24-II-82	363	362	460	98	27
2	26-X-80	30-IV-81	186	328	351	45	14
3	7-III-81	24-II-82	353	378	450	74	20
4	26-X-80	27-VIII-81	306	487	511	24	5
5	19-II-81	24-II-82	369	307	352	45	15
6	7-III-81	24-II-82	354	433	504	73	17
7	7-III-81	13-VII-82	492	393	492	56	14
		$\bar{x}$		381		62	17
		SD		58		24	7

[1]Eel No. 1 was captured four times; growth between first and third and between second and fourth captures were analyzed separately.

When the data are grouped into 50 mm size classes, animals in the 350-400 mm class grew faster than smaller animals (Fig. 1); 95% confidence intervals for other size classes overlapped, although some overlap may result from small samples of larger animals. Similar trends in relative growth (percent increase in length) were apparent (Fig. 1): values overlapped in the smaller size classes, and the largest size class grew slower than the fast-growing 350-400 mm group.

Growth rates during fast growth periods (Table 1) suggest that animals grew faster in 1982 than in 1981 (t-test, one tail, df = 76, $P < 0.05$). Maximum growth rates also differed: the 5 fastest growth rates, as well as 13 of the 15 fastest rates, occurred in 1982 (Table 1).

Information on weight gain is less complete but shows a similar seasonal trend. Average weight increase between recaptures was 0.223 g/d (SD = 0.222, $N = 47$) for the fast growth period; limited data suggest lesser gains for the slow growth period (0.017-0.144 g/d, $N = 2$). When seasonal data are summed and a 4-mo slow growth period is assumed, annual weight increase was 63 g. Long-term weight change data from two animals at large 299 and 371 d indicate an average weight increase of 76 g/yr (range = 67 to 86 g/yr).

Mean lengths at different ages were

Age class (yr):	*II*	*III*	*IV*	*V*	*VI*	*VII*
$\bar{x}$ length (mm)	242	310	361	403	442	460
Range (mm)	197-278	214-446	233-548	256-570	297-559	386-500
N	6	51	134	78	32	5

The mean values project an average annual increase of 44 mm (range = 39-68 mm). The related length-age regression for all eels aged at this locale during the study period was length = 183.3 + 43.5 × age ($N = 305$, $r = 0.492$, $P < 0.01$) which also projects an average annual increase of 44 mm (95% C.I. = ±8.7 mm) for an average eel 370 mm long.

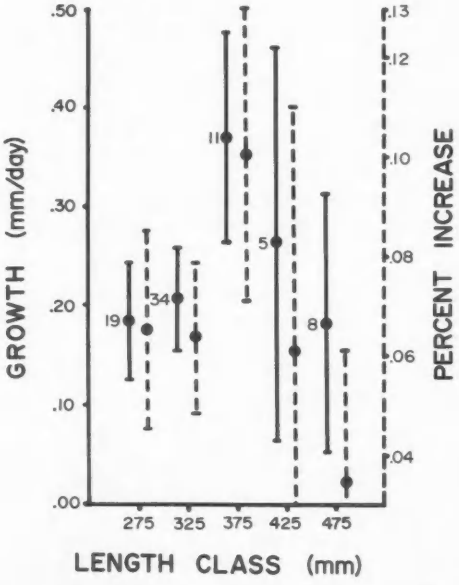

FIGURE 1.—Growth rates of recaptured American eels as a function of size at initial capture, Fridaycap Creek, Ga., October 1980-November 1982. Growth is expressed as the actual daily rate of increase (solid vertical lines, means ±95% confidence intervals) and the percent increase as a function of initial length (dashed vertical lines, means ±95% confidence intervals). Data are from fast growth periods, 1981 and 1982 combined. Numbers beside each mean are the total animals comprising each 50 mm size class. Midpoints of length classes are shown on x-axis.

Discussion

Comparisons of Growth Measures

Different procedures yielded different estimates of growth rate. The two independent, direct measures based on recaptures—seasonal summation and long-term recaptures—produced similar values (57 mm/yr and 62 mm/yr, respectively). The indirect measures—length-age regression and mean-length-at-age analysis—both projected annual growth rates of 44 mm/yr. All estimates are complicated by extreme variability in growth, with overlap in lengths among four to six year classes common (Smith and Saunders 1955; Ogden 1970; Gray and Andrews 1971; Hurley 1972). Growth rate estimates based on recapture data were apparently higher than those derived from length-at-age analyses, but confidence intervals overlapped among all estimates. However, we feel that the direct measures are more accurate. First, the sample size for the length-age analyses was more than three times larger than for the seasonal summation analysis, but the confidence intervals were very similar (17.4 mm and 17.8 mm, respectively), suggesting less variability in the recapture data. Second, growth rates derived from recaptured animals are based on actual growth between captures; variability in calculated growth rates should therefore reflect real variability in growth among animals. In length-age analyses, age classes are commonly resolved at no finer than an annual level. Consequently, growth subsequent to day 1 of each year increases the variance around the estimate rather than increasing the accuracy of the estimate. Finally, the accuracy of age determinations from otoliths in some eel populations is questionable (Moriarty and Steinmetz 1979; Deelder 1981; Casselman 1982), placing length-age analyses in doubt unless annulus formation can be verified.

Limited growth data from other mark-recapture studies of American eels are available. Hurley (1972) tagged 1,418 American eels in Lake Ontario, Canada, and reported recapture intervals for 13 large individuals (730-874 mm), which increased an average of 34 mm/yr. At two Louisiana freshwater locales, Gunning and Shoop (1962) tagged 43 American eels; only four recaptures provided usable data, indicating an average growth of 140 mm/yr (growth range = 46-325 mm, initial lengths = 255-915 mm). R. L. Haedrich[2] tagged 148 American eels in a Massachusetts estuary. Four individuals (initial lengths = 500-700 mm) had an average annual growth rate of 6% (range = 4.1-8.4%). An inverse latitudinal trend in growth is suggested (see also Harrell and Loyacano 1980), but direct comparison is complicated by different initial lengths, small sample sizes, and high variability in growth.

Length-related differences in growth have also been found for other populations. A shift from allometric to symmetric growth occurred at 800 mm for American eels in Lake Ontario (Hurley and Christie 1982). Those authors, as well as Smith and Saunders (1955), related such a growth change to physiological preparation for maturation and migration. Gray and Andrews (1971) found that American eels in New Brunswick, Canada, estuaries grew slowly after age XI. Helfman et al. (in press) suggested that maturation of Fridaycap Creek eels occurred at around age IV (mean length = 387 mm). An apparent decrease in growth rates of Fridaycap Creek animals longer than 400 mm (Fig. 1) supports their interpretation.

Causes of Seasonal Differences

Seasonal and annual differences in growth rate can be linked to fishing success as affected by climate. Eel fishing in Georgia estuaries is typically poor at water temperatures below 10°C and above 24°C. In 1980-81, estuarine water temperature fell below 10°C during December 1980, but average 1981-82 monthly temperatures were higher and did not reach the 10° minimum until January 1982. In addition, rainfall in 1981 was 45 cm below average, and mean water temperatures were 2°C higher during June through September than in 1982 (R. Arnsdorff[3] and T. E. Targett[4]). The winter slow growth period may therefore result from colder water temperatures and reduced feeding. Faster growth in 1981 than in 1982 may have resulted from elevated temperatures during much of the fast growth period of 1981. High water temperatures—leading to reduced feeding, interrupted growth, and poor fishing—occurs in European eels, *Anguilla anguilla* (Deelder 1981). Interrupted summer growth may

[2]R. L. Haedrich, Department of Biology, Memorial University of Newfoundland, St. John's, Newfoundland, Canada A1B 3X9, pers. commun. April 1983.

[3]R. Arnsdorff, Georgia Department of Natural Resources, Environmental Protection Division, 270 Washington St. S.W., Atlanta, GA 30334, pers. commun. October 1982.

[4]T. E. Targett, Skidaway Institute of Oceanography, P.O. Box 13687, Savannah, GA 31406, pers. commun. October 1982.

have occurred in our study population, but because we lack growth data from midsummer only, we cannot test for it.

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DESCRIPTION OF EARLY STAGE ZOEAE OF *SPIRONTOCARIS MURDOCHI* (DECAPODA, HIPPOLYTIDAE) REARED IN THE LABORATORY

Larvae of *Spirontocaris murdochi* Rathbun have not been described in the literature. During studies on rearing larvae in the laboratory for descriptive purposes, I succeeded in rearing zoeae of *S. murdochi* through Stage III. The first three zoeal stages of *S. murdochi* are described, illustrated, and compared with descriptions of morphologically similar hippolytid zoeae.

Methods and Rearing Results

I obtained an ovigerous female *Spirontocaris murdochi* carrying late-stage embryos while sampling pandalid shrimp in Auke Bay, Alaska, for toxicity studies. The female was caught 2 April 1979 at a depth of 18 m at lat. 58°21.6′ N, long. 134°39.3′ W. Stage I zoeae released from the female were reared in 250 ml jars containing about 200 ml of filtered seawater. The jars were checked daily for exuviae, and a few zoeae were preserved every other day. The zoeae were offered live plankton strained through a 0.333 mm mesh, but there was no evidence that the zoeae ate the plankton. (For a more complete description of the methods, see Haynes 1982.) Most of the zoeae molted to Stage II, but only two zoeae molted to Stage III.

Techniques of measurement and illustration are those of Haynes (1976, 1979). At least five zoeae of Stages I and II were used to verify segmentation and setation.

Description

The terms used in the descriptions and nomenclature of appendages are from Haynes (1976, 1979). Only those morphological characteristics useful for readily identifying each stage are given. Setation formulae are the number of setae per segment from the distal to the proximal segment. The telsonic setae are numbered as pairs beginning with the inner (medial) pair. For clarity, setules on setae are usually omitted, but spinulose setae are shown.

The following characteristics apply to zoeal Stages I, II, and III. The rostrum is slender, spiniform, without teeth, about one-fourth the length of the carapace, and projects horizontally. The ventral and posterior margins of the carapace are smooth except for pterygostomian spines. Mandibles are without palps; there is no proximal setose seta on the maxillule; and the maxillipeds are without epipodites. Abdominal somites 4 and 5 have posterolateral spines (the fifth pair is slightly longer than the fourth pair in Stage I, but both pairs are nearly the same length in Stages II and III). An anal spine is present.

Stage I Zoea

Mean total length of Stage I zoea (Fig. 1A), 3.4 mm (range 3.2-3.6 mm; six specimens). Eyes sessile. Carapace with two minute rounded prominences: One at posterior edge, other at base of rostrum.

ANTENNULE (Fig. 1B).—Protopodite of first antenna, or antennule, simple, unsegmented, tubular, with heavily plumose seta terminally. Conical projection tipped with four aesthetascs: Three long, one of intermediate length.

ANTENNA (Fig. 1C).—Second antenna, or antenna, with inner flagellum (endopodite) and outer antennal scale (exopodite). Flagellum unsegmented, slightly shorter than scale, styliform, tipped by plumose seta and shorter spine. Antennal scale distally divided into five joints (distal joint incomplete) and fringed with 10 heavily plumose setae along terminal and inner margins. Tip of antennal scale curved toward outer margin. Protopodite with spine only at base of flagellum.

MANDIBLES (Fig. 1D).—Incisor process of left mandible has four teeth in contrast to triserrate incisor process of right mandible. Both left and right mandibles with movable premolar denticle (lacinia mobilis). Left mandible with subterminal tooth.

MAXILLULE (Fig. 1E).—First maxilla, or maxillule, with coxopodite, basipodite, and endopodite. Coxopodite (proximal lobe) with seven spines: Five spinulose, two simple. Basipodite (median lobe) with 10 short, smooth spines terminally. Two-segmented endopodite originates from lateral margin of basipodite: Proximal segment with two spinulose spines, distal segment with three spinulose spines.

MAXILLA (Fig. 1F).—Second maxilla, or maxilla, has platelike exopodite (scaphognathite) with five plumose setae along outer margin and

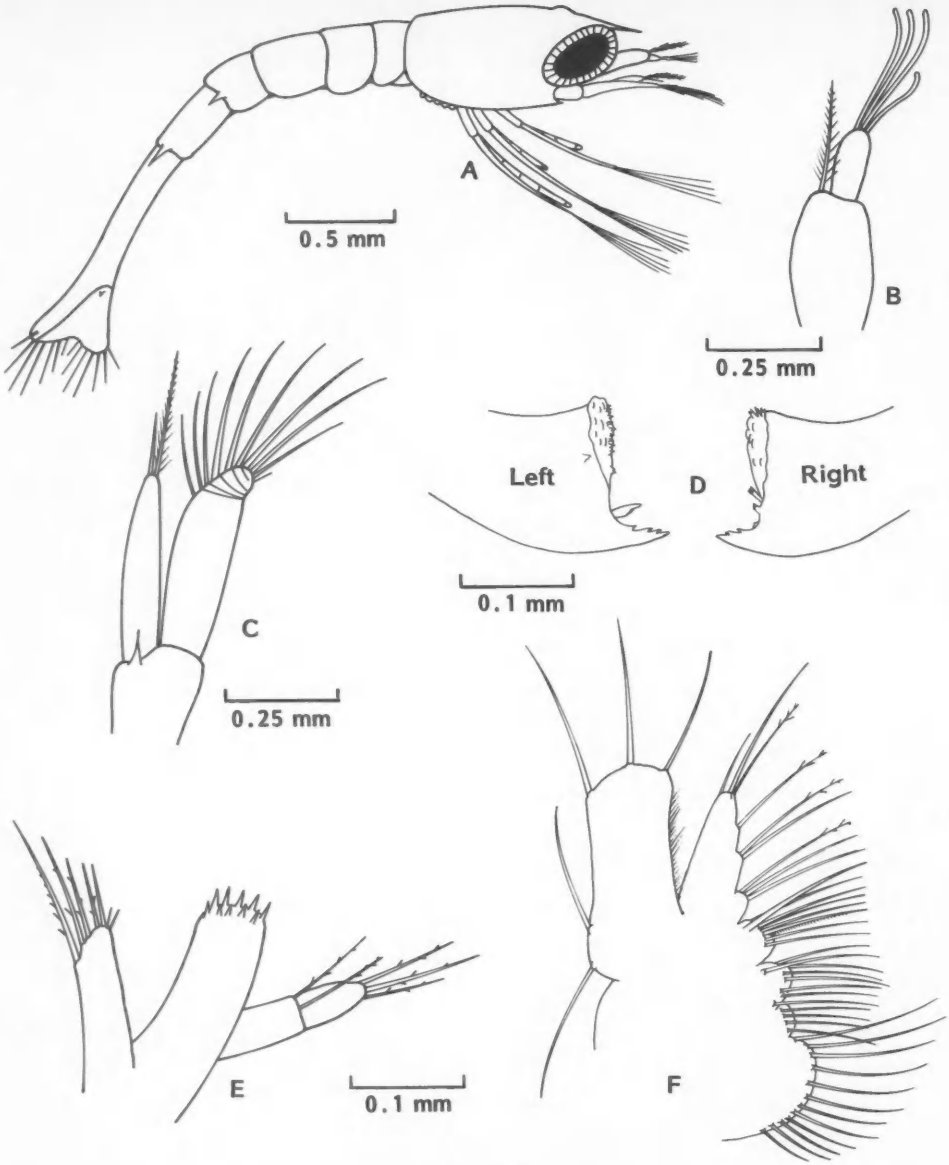

FIGURE 1.—Stage I zoea of *Spirontocaris murdochi*: A, whole animal, right side; B, antennule, dorsal; C, antenna, ventral; D, mandibles (left and right), posterior; E, maxillule, ventral; F, maxilla, dorsal.

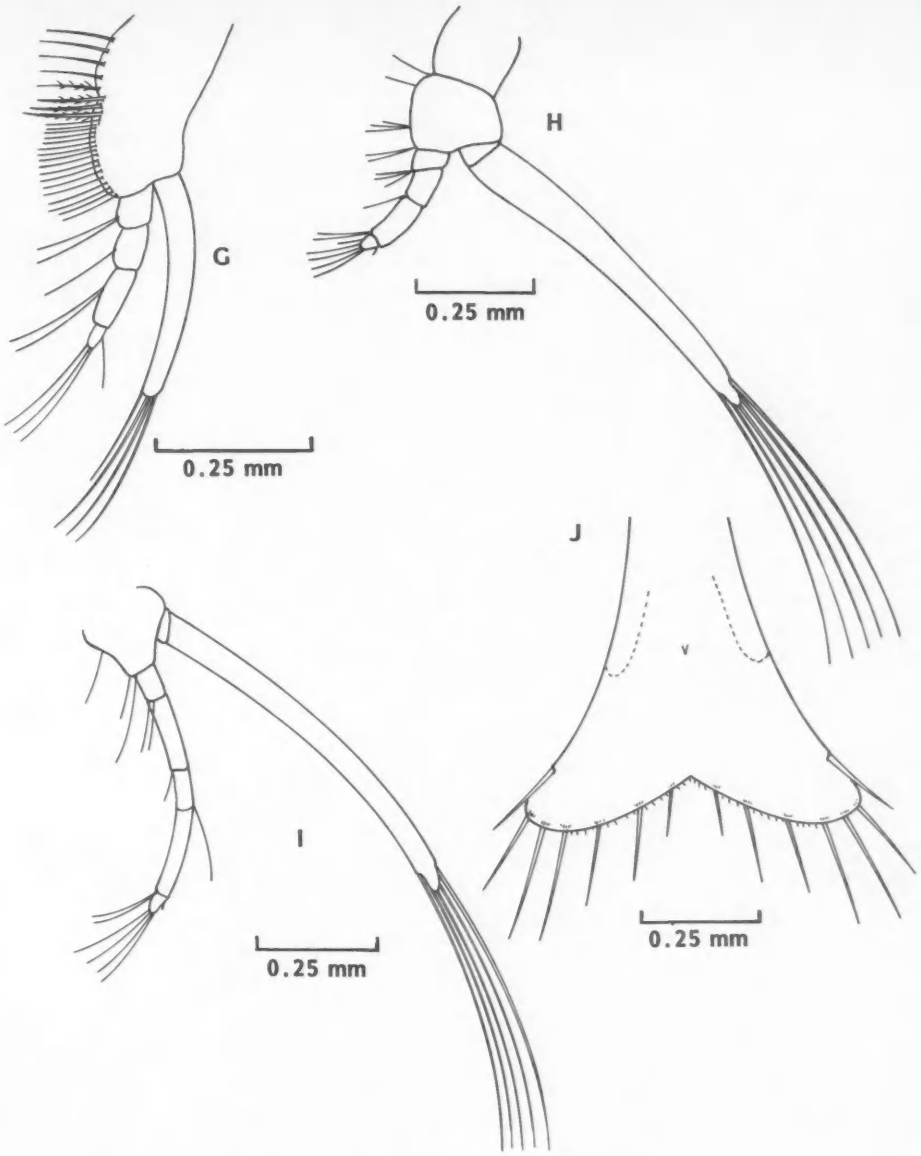

FIGURE 1.—*Continued*—G, first maxilliped, lateral; H, second maxilliped, lateral; I, third maxilliped, lateral; J, telson, ventral.

hairs along medial margin. Unsegmented endopodite with nine setae (four setae slightly spinulose). Coxopodite and basipodite bilobed. Coxopodite with eight setae on each lobe. Basipodite with 16 setae: 4 on distal lobe, 12 on proximal lobe.

FIRST MAXILLIPED (Fig. 1G).—Most setose of natatory appendages. Bilobed protopodite with 5 setae on proximal lobe, 20 setae on distal lobe (three of setae on distal lobe spinulose). Endopodite four-segmented; setation formula 4, 2, 1, 2. Exopodite (a long, slender ramus jointed at base) has four natatory setae.

SECOND MAXILLIPED (Fig. 1H).—Protopodite bisegmented: Distal segment with seven setae, proximal segment without setae. Endopodite four-segmented; setation formula 6, 2, 1, 3. Exopodite with five natatory setae.

THIRD MAXILLIPED (Fig. 1I).—Unsegmented protopodite with three setae. Five-segmented endopodite about two-thirds length of exopodite; setation formula 5, 2, 1, 1, 2. Exopodite with five natatory setae.

PEREOPODS.—Poorly developed, anteriorly directed under body.

PLEOPODS.—Absent.

ABDOMEN AND TELSON (Fig. 1A, J).—Abdomen with pair of posterolateral spines on somites 4 and 5, pair on somite 4 somewhat shorter than pair on somite 5. Telson emarginate posteriorly, fused with abdominal somite 6. Telson with 7 + 7 densely plumose setae, minute spinules at base of each seta except outermost pair, larger spinules along terminal margin of telson between bases of four inner pairs of setae. Uropods visible and enclosed.

Stage II Zoea

Mean total length of Stage II zoea, 3.7 mm (range 3.5-4.0 mm; three specimens). Eyes stalked. Carapace identical to Stage I carapace.

ANTENNULE (Fig. 2A).—Two-segmented, with large outer flagellum and smaller inner flagellum on terminal margin. Flagella not segmented; inner flagellum conical, with long spine terminally; outer flagellum with four aesthetascs terminally. Proximal segment with large spine projecting slightly downward from ventral surface. Both proximal and distal segments have two plumose setae each.

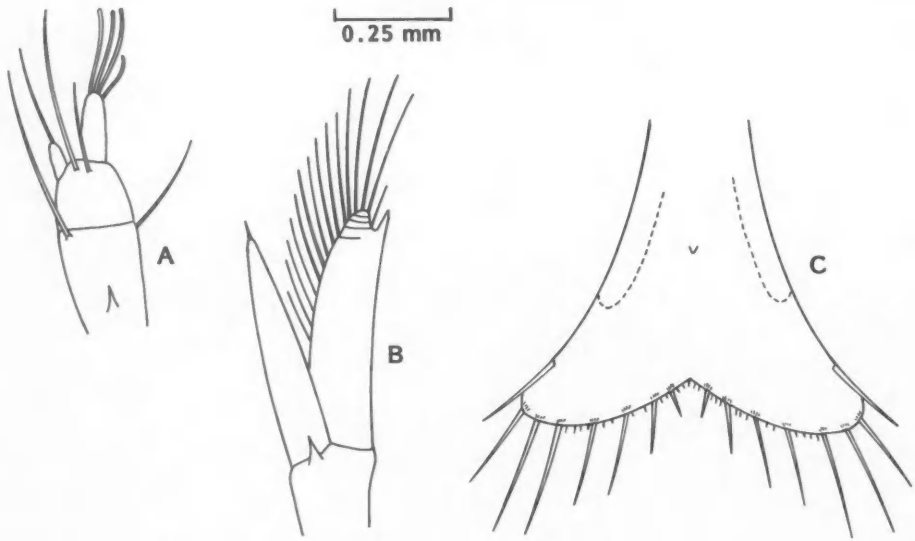

FIGURE 2.—Stage II zoea of *Spirontocaris murdochi*: A, antennule, ventral; B, antenna, ventral; C, telson, ventral.

ANTENNA (Fig. 2B).—Flagellum styliform, about same length as antennal scale, tipped by short spine. Antennal scale about 3.5 times as long as wide, fringed with 15 plumose setae along terminal and medial margins. Antennal scale with four joints distally (proximal joint incomplete), lateral projection on distal portion. Tip of antennal scale not curved laterally as in Stage I. Protopodite with spine at base of flagellum.

MANDIBLES.—Same as in Stage I except have slightly developed molar lip.

MAXILLULE, MAXILLA, AND MAXILLIPEDS.—Similar to Stage I except scaphognathite of maxilla has six setae; exopodites of maxillipeds 1-3 have 5, 8, and 10 natatory setae, respectively.

PEREOPODS.—Slightly larger than in Stage I, extend somewhat vertically, have naked exopodites on pereopods 1 and 2.

PLEOPODS.—Absent.

ABDOMEN AND TELSON.—Posterolateral spines on abdominal somites 4 and 5 nearly same length. Telson (Fig. 2C) still fused with abdominal somite 6, has 8 + 8 densely plumose setae. Enclosed uropods somewhat longer than in Stage I.

Stage III Zoea

Mean total length of Stage III zoea, 4.1 mm (range 3.9-4.3 mm; two specimens). Carapace identical to Stage II carapace, except has supraorbital spine.

ANTENNULE.—Similar to Stage II antennule except outer flagellum has subterminal seta, proximal segment with four setae around distal joint and three plumose setae laterally, distal segment with four large plumose setae.

ANTENNA, MANDIBLES, MAXILLULE, AND MAXILLA.—Similar to Stage II but with following differences. Antennal scale, without joints terminally, has 20 plumose setae along terminal and medial margins; subterminal spine extends just beyond tip of scale. Mandibles with a few additional teeth between incisor and molar processes. Maxillule with 9 spinulose spines on coxopodite and 12 short smooth spines on basipodite. Scaphognathite of maxilla has 9-12 plumose setae.

MAXILLIPEDS.—Exopodites of maxillipeds 1-3 have 5, 10, and 10 natatory setae, respectively.

PEREOPODS (Fig. 3A, B).—Exopodites only on pereopods 1 and 2; chelae present but undeveloped; endopodites of pereopods 1 and 2 with terminal seta.

PLEOPODS.—Present as buds.

ABDOMEN AND TELSON.—Telson (Fig. 3C),

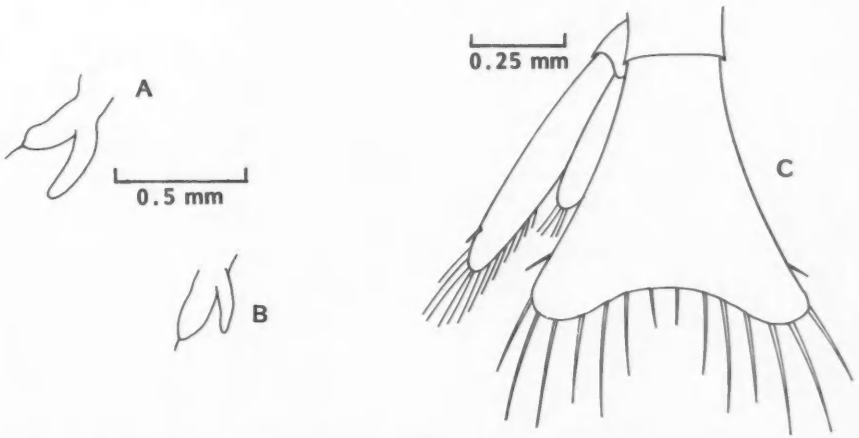

FIGURE 3.—Stage III zoea of *Spirontocaris murdochi*: A, pereopod 1, lateral; B, pereopod 2, lateral; C, telson, dorsal.

jointed with abdominal somite 6, has 8 + 8 densely plumose setae. Most of spinules at setal bases and along terminal margin absent. Uropods free. Endopodite of uropod about one-half length of exopodite, has four setae along terminal margin. Exopodite usually with 13 distal marginal setae and an outer subterminal spine.

Comparison of Zoeal Stages with Descriptions by Other Authors

Of the described *Spirontocaris* zoeae, those of *S. murdochi* are most similar to zoeae of *S. spinus* (Sowerby), *S. spinus intermedia* Makarov, and *S. phippsii* (Krøyer): all have relatively long, spiniform rostrums; exopodites on pereopods 1 and 2; and posterolateral spines on abdominal somites 4 and 5. However, larvae of *S. spinus* (described by Pike and Williamson 1961) and *S. spinus intermedia* (described by Ivanov 1971) are distinguishable from larvae of *S. murdochi*: *S. spinus* and *S. spinus intermedia* have a tuft of setae on the dorsal surface of abdominal somite 4; *S. murdochi* does not. Furthermore, in Stage I zoeae of *S. spinus* and *S. spinus intermedia*, the posterolateral spine on abdominal somite 5 is as short as, or shorter than, the spine on abdominal somite 4; whereas, in Stage I zoeae of *S. murdochi*, the posterolateral spine on abdominal somite 5 is noticeably longer than the posterolateral spine on abdominal somite 4.

Pike and Williamson (1961) described a Stage II specimen of *S. phippsii* whose identity is assumed from the distribution of adults in the northwestern Atlantic Ocean. The specimen is described as being nearly the same as Stage II *S. spinus* except somewhat larger (6.0 mm). Also, the posterolateral spines on abdominal somites 4 and 5 of *S. phippsii* are "more prominent", the dorsal tuft of setae on abdominal somite 4 is absent, the telson is "broader", and the second pair of telsonic spines are about three-fourths the length of the third pair. This description is inadequate to distinguish between Stage II *S. phippsii* and Stage II *S. murdochi*, except for total length: Stage II *S. murdochi* average 3.7 mm total length compared with 6.0 mm for *S. phippsii*.

The Stage III zoeae described as "*Spirontocaris* larva Nr. 2" by Stephensen (1916) from Greenland waters are assumed to be *S. phippsii* (Pike and Williamson 1961). When the figures and description of Stephensen's Stage III zoeae are compared with my description of Stage III *S. murdochi*, *S. murdochi* are smaller and noticeably less developed. Stephensen's zoeae are 6.5 mm long, the carapace has an antennal spine, the pleopods and the chelae of pereopods 1 and 2 are clefted, and telsonic setal pairs 3 and 4 are the same length. My Stage III zoeae average 4.1 mm long, the carapace does not have antennal spines, the pleopods and chelae of pereopods 1 and 2 are not clefted, and the third pair of telsonic setae are noticeably shorter than the fourth pair of telsonic setae.

It should be noted, however, that this comparison of zoeae of *S. murdochi* and *S. phippsii* is based on specimens from different geographical areas as well as specimens of *S. phippsii* that are of unproven identity. Confirmation of morphological development of *S. phippsii* larvae from the North Pacific Ocean is desirable.

Acknowledgment

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INCIDENCE OF MOLTING AND SPAWNING IN THE SAME SEASON IN FEMALE LOBSTERS, *HOMARUS AMERICANUS*

The reproductive cycle in female lobsters, *Homarus americanus*, normally covers 2 yr. Molting and mating occur first, primarily during the summer months. Laying of eggs (spawning) takes place about a year later. Hatching of eggs, followed by molting and mating again, takes place another year later (Aiken and Waddy 1980). However, departures from the normal cycle occur. One such departure is molting and egg laying in the same year (Aiken and Waddy 1980; Ennis 1980). Ennis (1980) noted that new-shelled ovigerous females obtained in fall sampling at various Newfoundland localities ranged towards the lower end of the size range of all ovigerous specimens and suggested that those females that molt and spawn in the same year are spawning for the first time. Aiken and Waddy (1980) similarly suggested that this phenomenon probably occurs primarily in the Adult-I year (i.e., first spawning).

In this paper I present data on the incidence of this phenomenon in a Newfoundland lobster population and illustrate its relationship to size of lobster.

Materials and Methods

Annually, since 1975, research fishing for lobsters has been carried out in autumn, following the summer molting/spawning period, in the area of Arnold's Cove, Placentia Bay, on the southeast coast of Newfoundland. The main purpose of this fishing is to tag legal lobsters to obtain estimates of standing stock during the following spring fishing season. All lobsters caught are measured, sexed, and examined for shell condition to determine whether molting has occurred recently and for the presence of external eggs. Since hatching of eggs laid the previous year occurs during July-August in this area, all ovigerous specimens present in the autumn carry recently laid eggs.

To determine the relationship between percent molting and laying eggs in the same season, it was necessary to convert the observed postmolt carapace length (CL) of new-shelled ovigerous specimens to premolt carapace length. This was done using a premolt-postmolt carapace length relationship for Arnold's Cove lobsters (Ennis 1978). The data for all years were pooled. The total number of ovigerous specimens examined and the number which had molted prior to laying eggs at each 1 mm CL interval (premolt carapace length for new-shelled specimens) were subjected to probit analysis.

Results and Discussion

All ovigerous lobsters ≤70 mm CL (premolt) molted prior to laying eggs. Beyond 70 mm, the percentage of animals that molt and lay eggs in the same season declined very rapidly to zero at 82 mm CL (Fig. 1).

The lobsters in which Aiken and Waddy (1976, 1980) noted the occurrence of molting and egg laying in the same individual during the same molting/spawning season came from the southern Gulf of St. Lawrence. They suggested that the high summer water temperatures that prevail in the area may be the cause of the phenomenon. However, its occurrence in several Newfoundland localities (Ennis 1980) indicates that the phenomenon may be quite widespread.

At Arnold's Cove the percentage of non-ovigerous females that molt and lay eggs in the same season declines to zero over the size range (70-82 mm CL) where functional maturity increases to 50% (Ennis 1984). This is consistent with the suggestion that this phenomenon occurs in animals laying eggs for the first time. If this is so, the incidence of this phenomenon in a population is likely to be related to the minimum legal

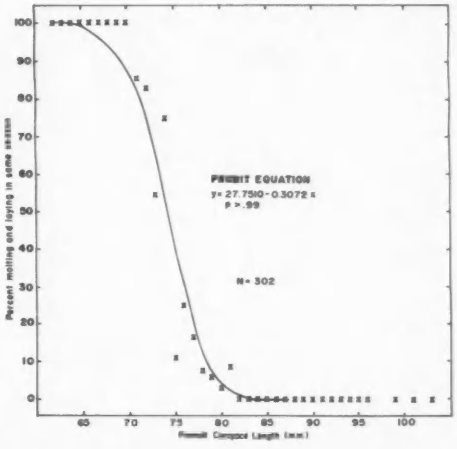

FIGURE 1.—Percentage of non-ovigerous female lobsters that molt and lay eggs in the same season in relation to size at Arnold's Cove, Newfoundland.

size (in relation to size at maturity) and exploitation rates in the fishery. In a fishery with a small minimum legal size and high exploitation rates, most of the ovigerous females in the population would be small animals laying for the first time.

The incidence of new-shelled ovigerous females in autumn sampling at Arnold's Cove has ranged from 0 to 38.5% of the total ovigerous specimens examined (Table 1). This year-to-year variability, which has also been observed elsewhere in Newfoundland (Ennis 1980), could be accounted for by variation in relative abundance of prerecruit animals caused by annual fluctuation in recruitment and exploitation rate.

TABLE 1.—Percentage of ovigerous lobsters with new shells in autumn sampling at Arnold's Cove, Newfoundland, 1975-82.

Year	No. ovigerous examined	% ovigerous with new shell	Carapace length (mm)	
			Range of ovigerous	Range of new-shelled ovigerous[1]
1975	75	10.7	72-103	73-83
1975[2]	16	12.5	65-92	65-71
1976	31	6.5	73-92	83-90
1976[2]	26	19.2	68-91	68-77
1977	78	38.5	71-101	76-88
1978	12	16.7	71-95	82-83
1979	31	25.8	72-99	72-90
1980	18	0.0	73-99	—
1981	31	6.5	71-101	71-81
1982	27	3.7	75-94	75

[1]These are postmolt carapace lengths.
[2]Diver-caught samples obtained during the same period as the trap-caught samples.

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PARASITES OF OLIVE ROCKFISH, *SEBASTES SERRANOIDES*, (SCORPAENIDAE) OFF CENTRAL CALIFORNIA

The olive rockfish, *Sebastes serranoides*, inhabits reefs from Del Norte County, Calif., to San Benito Island, Baja California, Mexico. Olive rockfish are large (to 64 cm TL), active predators, usually found in the water column, but occasionally hovering over or resting upon rocky substrates. Juveniles are primarily midwater feeders, preying upon zooplankton and small fishes, though some demersal feeding (e.g., isopods, caprellid and gammarid amphipods, etc.) has been noted (Hobson and Chess 1976; Love and Ebeling 1978; Love and Westphal 1981). Adults feed almost entirely on nektonic forms of squid and fish and on substrate-dwelling octopus (Love and Westphal 1981).

Little is known about the parasite fauna of olive rockfish, as previous reports are either descriptions of newly discovered species (Cressey 1969; Moser and Love 1975; Love and Moser 1976; Moser et al. 1976) or surveys of particular parasites throughout a fish community (Turner et al. 1969; Hobson 1971; Dailey et al. 1981). As part of a life-history study, we investigated the parasite population of central California olive rockfish.

Methods

Specimens were collected monthly from April 1975 to February 1976 at a group of shallow-water pinnacles, about 11 km west of Avila Beach, San Luis Obispo Co., Calif., (Fig. 1). These pinnacles, at depths of 20-30 m, are situated 100-300 m offshore from Diablo Cove and North Cove and rise to within 5-10 m of the surface.

Six hundred olive rockfish, ranging from 8.6 to 49.2 cm TL, were collected by hook and line or spear, placed in plastic bags, and frozen for later dissection. After thawing, each specimen was

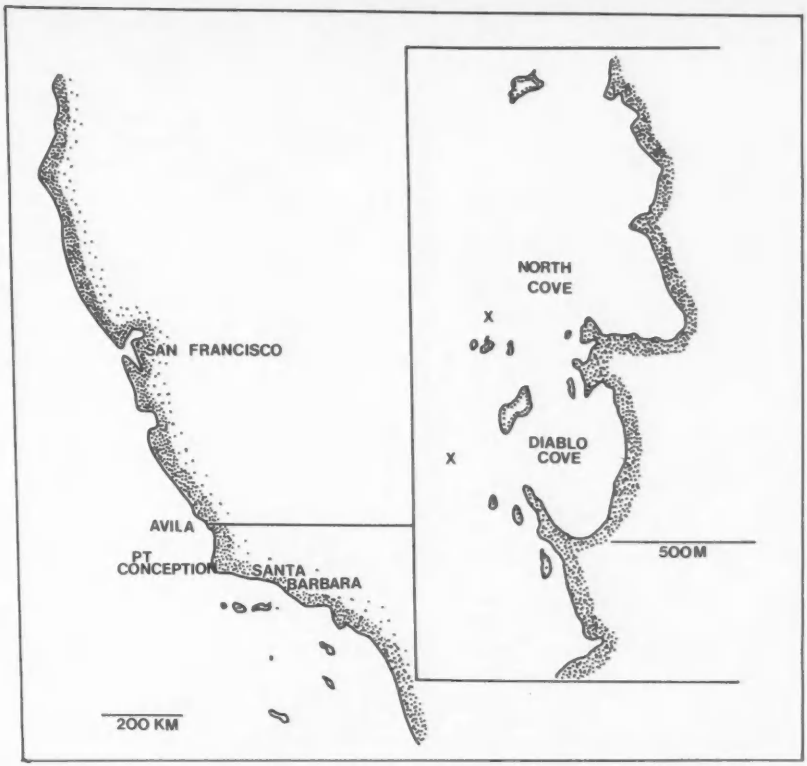

FIGURE 1.—Location of sampling sites (marked with x) for olive rockfish off Diablo Cove, Calif.

measured (total length) to the nearest millimeter and examined for parasites on external surfaces, gills, gill cavities, mouth, mesentery, heart, gallbladder, stomach, intestine, and muscle. Copepods and monogenetic and digenetic trematodes were fixed in alcohol-formaldehyde-acetic acid (AFA). The trematodes were stained with Harris' hematoxylin, cleared with xylene, and mounted. Nematodes were cleared in lactophenol. Protozoans were studied unpreserved after thawing.

Most parasites were identified to the lowest possible taxon. However, the microsporida, copepods of the genera *Caligus* and *Lepeophtheirus*, and larval cestodes, nematodes, and acanthocephalans were not identified to species. Copepods of the genera *Caligus* and *Lepeophtheirus* were only identified to genus, as an earthquake destroyed most of the specimens before they were identified to species.

To facilitate our analysis, we grouped together the relatively uncommon gallbladder myxozoans (= myxosporidans) (*Ceratomyxa sebasta, Leptotheca informis, L. longipes, L. macrospora, Myxidium incurvatum, Zschokkella ilishae*) and the hemiurid trematodes (*Lecithaster gibbosus, Parahemiurus merus, Lecithochirium exodicum*, and *Tubulovesicula lindbergi*).

We analyzed the incidence of infection of all parasites over the entire range of host lengths throughout the year. Differences in prevalence between size classes and between monthly samples were examined using the Kruskal-Wallis test.

Results

For our analyses we divided the specimens into 11 size classes. Table 1 shows the number of specimens taken per month per size class.

TABLE 1.—The number of olive rockfish taken per month per size class, April 1975-February 1976.

Month	Size class (cm TL)									
	5-10	11-15	16-20	21-25	26-30	31-35	36-40	41-45	46+	Total
April	6	6	3	6	8	10	6	7	3	55
May	4	7	4	4	5	8	8	8	4	52
June	5	5	5	8	6	9	5	7	6	56
July	6	5	7	8	6	8	9	8	7	64
Aug.	4	4	7	6	10	8	7	6	5	57
Sept.	5	8	6	9	5	9	9	9	3	63
Oct.	4	7	5	4	8	7	10	5	4	54
Nov.	5	6	5	6	7	8	8	7	3	55
Dec.	4	6	6	5	7	11	8	8	5	60
Jan.	2	3	5	6	4	6	6	7	5	44
Feb.	2	1	6	4	5	8	6	4	4	40
Total	47	58	59	66	71	52	82	76	49	600

Thirty-six parasite species were recovered from olive rockfish (Table 2). Five species were found in <1% of the individuals examined. These incidental parasites were an unidentified microsporidan and the copepods *Neobrachiella robusta, Chondracanthus pinguis, Naobranchia occidentalis*, and *Sarcotaces arcticus*. Found in <10% of the hosts were *Davisia reginae, Kudoa clupeidae, Leptotheca longipes*, and *L. macrospora* (Myxozoa); *Trochopus marginata* (Monogenea); *Aporocotyle macfarlani, Lecithaster gibbosus, Lecithochirium exodicum, Parahemiurus merus*, and *Tubulovesicula lindbergi* (Digenea); *Anisakis* sp. and *Phocanema* sp. (Nematoda); *Caligus* sp. and *Clavella parva* (Copepoda); and Rhabinorhynchidae gen. sp. (Acanthocephala).

Larval cestodes were the most commonly encountered parasites, infecting 98% of all individuals >20 cm in length. Larval *Contracaecum* sp. were found in 62% and cysticanths of immature *Corynosoma* sp. in 18% of fishes >20 cm.

Of parasites which use *Sebastes serranoides* as a final host, *Microcotyle sebastis* had the highest prevalence, occurring on more than 90% of hosts >20 cm. It was most prevalent on the filaments of the first gill arch (Table 3), declining in number through successive arches ($\chi^2 = 108.1, P < 0.001$). No significant differences in infection intensities were noted between left and right arches.

Other commonly encountered ectoparasites were *Holobomolochus spinulus, Neobenedenia girellae*, and *Lepeophtheirus* sp. Adult metazoan endoparasites were not abundant, though three, *Deretrema cholaeum, Opechona sebastodis*, and *Hysterothylacium aduncum*, were often found in larger fish.

Three myxozoans, *Henneguya sebasta, Leptotheca informis*, and *Zschokkella ilishae*, were found in more than 10% of hosts. *Henneguya sebasta* was found in 93% of hosts >35 cm. Nine percent of *H. sebasta* infections were sufficiently severe to virtually occlude the bulbous arteriosus. Although no histological sections were made, no evidence of gross pathogenic effects were noted, as these heavily infected individuals were of an age and weight indistinguishable statistically (analysis of variance) from lightly or non-infected individuals.

TABLE 2.—Parasites recovered from olive rockfish, *Sebastes serranoides*, off Diablo Cove, Calif. *denotes first host records.

Parasite	Location
Protozoa (Myxozoa)	
Ceratomyxa sebasta	Gallbladder
Davisia reginae	Urinary bladder
Henneguya sebasta	Bulbus arteriosus, gallbladder (rarely)
**Kudoa clupeidae*	Muscle
Leptotheca informis	Gallbladder
Leptotheca longipes	Gallbladder
Leptotheca macrospora	Gallbladder
Myxidium incurvatum	Gallbladder
Zschokkella ilishae	Gallbladder
*Protozoa (Microsporida)	Urinary bladder
Monogenea	
**Microcotyle sebastis*	Gills
**Neobenedenia girellae*	Skin, mouth
**Trochopus marginata*	Gills
Digenea	
**Aporocotyle macfarlani*	Afferent branchial arteries
**Deretrema cholaeum*	Gallbladder
**Lecithaster gibbosus*	Stomach
**Lecithochirium exodicum*	Stomach
**Opechona sebastodis*	Intestine
**Parahemiurus merus*	Stomach
**Podocotyle* sp.	Stomach
**Tubulovesicula lindbergi*	Stomach
Cestoda	
*Tetraphyllidea (immature)	Viscera
Nematoda	
Anisakis sp. (immature)	Viscera
**Contracaecum* sp. (immature)	Viscera
**Hysterothylacium (=Thynnascaris) aduncum*	Stomach, intestine
Phocanema sp. (immature)	Muscle
Copepoda	
**Neobrachiella robusta*	Gills
Caligus sp.	Skin, gills
**Chondracanthus pinguis*	Gills
**Clavella parva*	Dorsal and anal fin rays
Holobomolochus spinulus	Gills, inner surface of gill opercula
**Lepeophtheirus* sp.	Skin, gills
**Naobranchia occidentalis*	Gills
**Sarcotaces arcticus*	Body cavity near anus
Acanthocephala	
**Corynosoma* sp. (immature)	Viscera
**Echinorhynchus gadi*	Intestine
*Rhabdinorhynchidae gen. sp.	Intestine

TABLE 3.—Position and number of *Microcotyle sebastis* on 32 olive rockfish, *Sebastes serranoides*, off Diablo Cove, Calif.

Arch number	Arch position		Total
	Left	Right	
1	114	124	238
2	60	63	123
3	29	37	66

We found numerous cases of multiple species myxozoan infections in the gallbladder, particularly in individuals >35 cm. Twenty-two percent of all infections were comprised of two species, 5.1% of three, and 1.2% of four. The occurrence of myxozoans in *Deretrema cholaeum*-infected gallbladders occurred less frequently than expected ($\chi^2 = 123.3$, $P < 0.0001$).

The species of parasites infecting olive rockfish by host length and age is shown in Table 4. *Sebastes serranoides* harbors a maximum number of parasite species between 31 and 40 cm or 4 and 10 yr of age [compared with 3-6 yr in *S. alutus* and *S. caurinus* (Sekerak 1975)]. Of the five species of parasites found in the smallest size class, four exhibited direct life cycles, whereas in fish of 20 cm (1-2 yr old) 6 of 11 species had indirect life cycles. In the largest class (41-50 cm), slightly less than half (15 of 34) of the species had indirect life cycles. By 20 cm, representatives of all the parasite groups, with the exception of microsporida, were found in olive rockfish. The prevalence rates of six parasite species and one parasite group increased significantly with increasing host length (Fig. 2). Seven species or species groups showed significant annual changes in prevalence (Fig. 3).

Discussion

Of the seven parasite species showing increasing prevalence with increasing host length, six (*Lepeophtheirus* sp., *Neobenedenia girellae*, *Microcotyle sebastis*, *Holobomolochus spinulus*, *Henneguya sebasta*, and the gallbladder myxozoans) had direct life cycles and one (*Hysterothylacium aduncum*) had an indirect cycle. A change in diet to-

TABLE 4.—Parasite species infecting five size classes of olive rockfish off Diablo Cove, Calif. See Table 1 for number of specimens per size class.

Host length cm TL (age in years)				
5-10 (0)	11-20 (1-2)	21-30 (1-4)	31-40 (4-10)	41-50 (7-20)
	Acanthocephala	Acanthocephala	Acanthocephala	Acanthocephala
	Corynosoma sp.	*Corynosoma* sp.	*Corynosoma* sp.	*Corynosoma* sp.
		Rhabdinorhynchidae gen. sp.	Rhabdinorhynchidae gen. sp.	Rhabdinorhynchidae gen. sp.
Cestoda	Cestoda	Cestoda	Cestoda	Cestoda
Tetraphyllidea	Tetraphyllidea	Tetraphyllidea	Tetraphyllidea	Tetraphyllidea
Copepoda	Copepoda	Copepoda	Copepoda	Copepoda
N. robusta	*H. spinulus*	*Caligus* sp.	*Caligus* sp.	*Caligus* sp.
C. parva	*Lepeophtheirus* sp.	*H. spinulus*	*C. pinguis*	*C. pinguis*
N. occidentalis		*Lepeophtheirus* sp.	*H. spinulus*	*H. spinulus*
		S. arcticus	*Lepeophtheirus* sp.	*Lepeophtheirus* sp.
			N. occidentalis	*N. occidentalis*
			S. arcticus	*S. arcticus*
	Digenea	Digenea	Digenea	Digenea
	D. cholaeum	*D. cholaeum*	*A. macfarlani*	*A. macfarlani*
	O. sebastodis	*L. gibbosus*	*D. cholaeum*	*D. cholaeum*
		L. exodicum	*L. gibbosus*	*L. gibbosus*
		O. sebastodis	*L. exodicum*	*L. exodicum*
		P. merus	*O. sebastodis*	*O. sebastodis*
		Podocotyle sp.	*P. merus*	*P. merus*
		T. lindbergi	*Podocotyle* sp.	*Podocotyle* sp.
			T. lindbergi	*T. lindbergi*
Monogenea	Monogenea	Monogenea	Monogenea	Monogenea
M. sebastis	*M. sebastis*	*M. sebastis*	*M. sebastis*	*M. sebastis*
	N. girellae	*N. girellae*	*N. girellae*	*N. girellae*
		T. marginata	*T. marginata*	*T. marginata*
	Nematoda	Nematoda	Nematoda	Nematoda
	Contracaecum sp.	*Anisakis* sp.	*Anisakis* sp.	*Anisakis* sp.
	H. aduncum	*Contracaecum* sp.	*Contracaecum* sp.	*Contracaecum* sp.
		H. aduncum	*H. aduncum*	*H. aduncum*
			Phocanema sp.	*Phocanema* sp.
	Protozoa (Myxozoa)	Protozoa (Myxozoa)	Protozoa (Myxozoa)	Protozoa (Myxozoa)
	H. sebasta	*C. sebasta*	*C. sebasta*	*C. sebasta*
		H. sebasta	*D. reginae*	*D. reginae*
		K. clupeidae	*H. sebasta*	*H. sebasta*
		L. informis	*K. clupeidae*	*K. clupeidae*
		L. longipes	*L. informis*	*L. informis*
		L. macrospora	*L. longipes*	*L. macrospora*
		M. incurvatum	*L. macrospora*	*L. sebasta*
		Z. ilishae	*L. sebasta*	*M. incurvatum*
			M. incurvatum	*Z. ilishae*
			Z. ilishae	
		Protozoa (Microsporida)	Protozoa (Microsporida)	Protozoa (Microsporida)
Total number of specimens:				
5	11	29	35	34

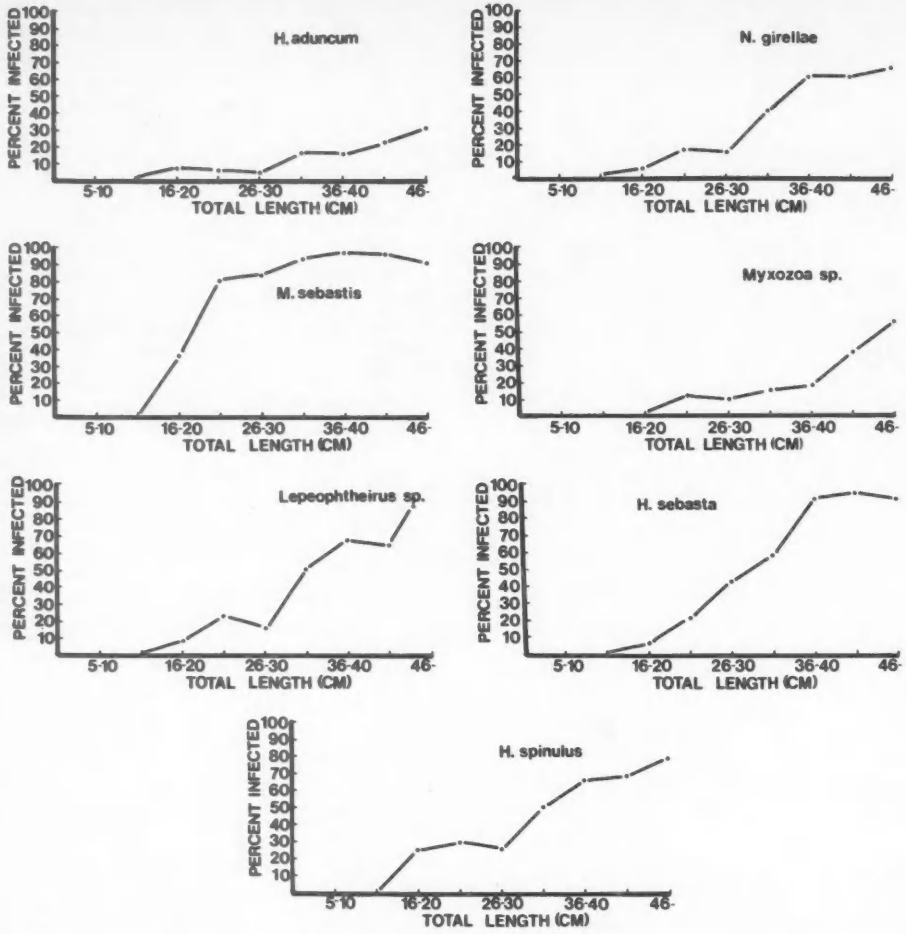

FIGURE 2.—The relationships between host length and percent prevalence of infection by seven parasite species from olive rockfish taken off Diablo Cove, Calif. All relationships show significant difference at $P \leq 0.05$. See Table 3 for numbers of fish examined in each length interval; see Table 1 for the number of specimens per size class.

ward fish and away from zooplankton (Love and Westphal 1981) probably accounts for the increase in *Hysterothylacium aduncum* infections, as fish are thought to be intermediate hosts for this species (Margolis 1970). The prevalence of *Clavella parva* was the opposite—it was found only in hosts <10 cm in length. *Clavella parva* attaches to dorsal, anal, and caudal fin rays. Perhaps structural barriers (such as ray diameter or surface characteristics) or increased water flow over the fins in larger fish prevent infection. Similar infection patterns were noted in *Sebastes alutus* and *S. caurinus* by Sekerak (1975).

Among species with seasonal patterns of infection, winter maximum infections were exhibited by *Lepeophtheirus* sp., *Holobomolochus spinulus*, the gallbladder myxozoans, and *Deretrema cholaeum*. The first three forms listed have direct life cycles. Olive rockfish are winter and early spring spawners (December-March) with internal fertilization occurring from November to February. It is possible that these parasites time their

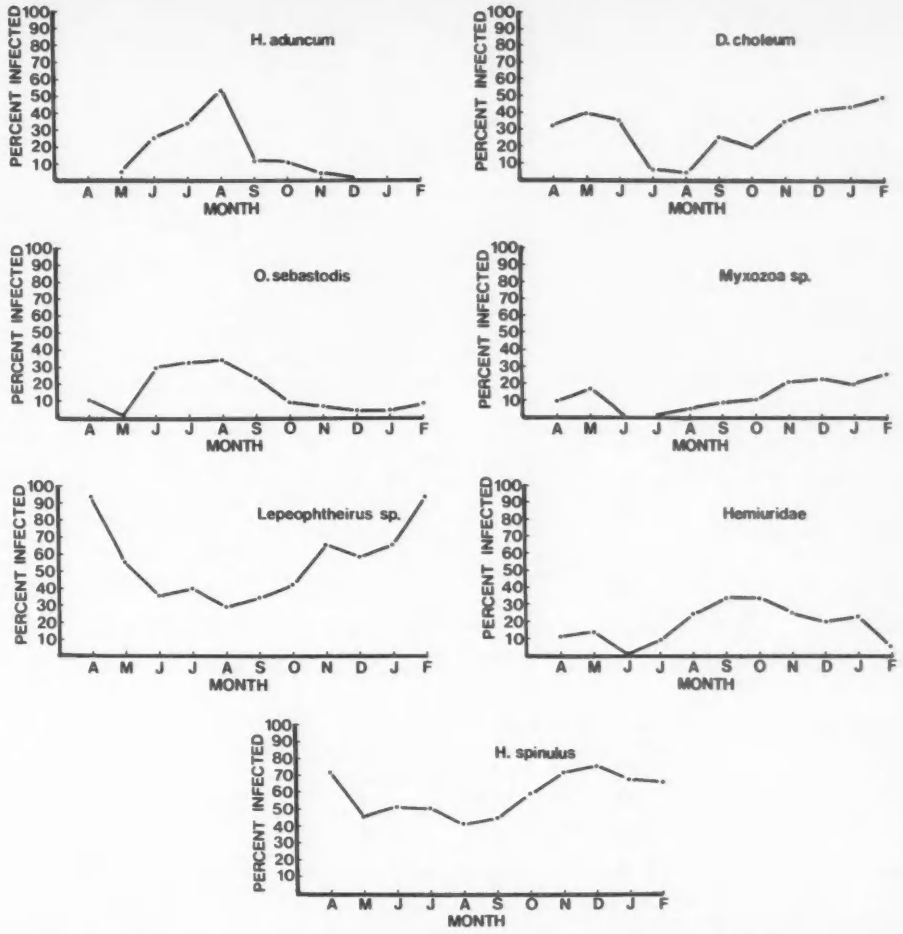

FIGURE 3.—The relationships between month of capture and percent prevalence of infection by seven parasite species from olive rockfish taken off Diablo Cove, Calif. All relationships show significant differences at $P \leq 0.05$. See Table 1 for the number of specimens per month.

movements and reproduction to coincide with that period when their hosts may be at closest proximity with each other. This phenomenon was observed between the Monogenea, *Dactylogyrus vastator* and *Mazocraes alosae*, and their respective hosts, *Cyprinus carpio* and *Alosa sapidissima* (Kennedy 1975).

Parasites with maximum prevalence during other periods all had indirect life cycles. The hemiurid trematode infections peaked in autumn, *Opechona sebastodis* in summer, and *Hysterothylacium aduncum* was most abundant in April and August. Seasonality among hemiurids has been reported by Shotter (1973) in whiting, *Odontogadus merlangus*, of the Irish Sea and in staghorn sculpin, *Leptocottus armatus*, from Oregon by Burreson and Olson (1974). In both cases infections were greatest in late summer or early fall.

The infection patterns we observed may reflect differences in the oceanographic conditions off central California. Water conditions in this region

may be divided into two periods (Bakun 1973), "upwelling" (March-August) and "oceanic" (September-February). Upwelling periods are characterized by an increase in the flow of nutrient-rich bottom water to the surface and increased plankton abundance. Olive rockfish food habits change with these seasons (Love and Westphal 1981). Zooplankton (particularly pelagic tunicates and euphausids), squids, and juvenile rockfish are eaten in greater quantity during the upwelling season, due to increased availability.

The secondary intermediate hosts for hemiurids and *Opechona sebastodis* are planktonic (Shotter 1973; Yamaguti 1971), and the prevalence increase may be due to greater seasonal predation on the planktonic intermediate host. Similarly, as fish are possible intermediate hosts of *Hysterothylacium aduncum*, its infection pattern may reflect the rockfish's heavy predation on juvenile rockfish during the upwelling period.

All of the parasite species infecting olive rockfish infect at least some other rockfish species. The genus *Sebastes* has exhibited an explosive radiation in the northeast Pacific (Kabata 1970). This rapid speciation has occurred relatively recently, probably during and after the Miocene[1]. Despite extreme morphological and behavioral differences between species, there is little species specificity among rockfish parasites, perhaps because of the rapidity of the host speciation events. Eighty-nine adult metazoan parasites have been reported from rockfishes between Alaska and California (Love and Moser 1983). Of these, 30 species have been found to infect only *Sebastes* spp. and 10 of the 89 species were unique to one host species.

Some of this specificity may be a function of host behavior or habitat preference rather than physiological differences (Kennedy 1975) between rockfish hosts. Holmes (1971) found that a rockfish's proximity to rocky reefs influenced the prevalence of the digenetic trematodes *Psettarium sebastodorum* and *Aporocotyle macfarlani*. *Aporocotyle macfarlani* was found in species associated with inshore reefs, *P. sebastodorum* in those hosts living away from rocks or in deeper waters. Olive rockfish, limited to relatively shallow reefs, occasionally harbored *A. macfarlani* but was not infected with *P. sebastodorum*.

Some parasites, particularly ectoparasites, are widespread among rockfishes. For example, *Microcotyle sebastis* has been reported from 22 species, *Naobranchia occidentalis* from 13, *Neobranchiella robusta* from 21, and *Chondracanthus pinguis* from 19. These and other parasites exhibit an extensive latitudinal range, considerably longer than some of their hosts. Further surveys of those species only lightly studied (such as *Sebastes eos, S. melanostomus, S. mystinus, S. rastrelliger*, and *S. semicinctus*) will show that some of those parasites infect nearly all rockfish species.

[1]W. Eschmeyer, California Academy of Science, Golden State Park, San Francisco, CA, pers. commun. 1982.

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SENSITIVITY OF THE POPULATION GROWTH RATE TO CHANGES IN SINGLE LIFE HISTORY PARAMETERS: ITS APPLICATION TO *MYA ARENARIA* (MOLLUSCA:PELECYPODA)

The question of sensitivity analyses in demographic studies was first addressed by Lewontin (1965), and since that time, Hamilton (1966), Demetrius (1969), Emlen (1970), Goodman (1971), Keyfitz (1971), and Mertz (1971) have made contributions in the area. More recently, Caswell (1978) has given general formulae for the sensitivity of the population growth rate (λ) derived from a Leslie model, to changes in single life history parameters written as formulae involving eigenvectors of the Leslie matrix. The application of such analyses to the study of the population dynamics of commercially important species can provide useful information to those interested in resource management.

The work presented here describes the sensitivity of the population growth rate to changes in the settlement rate (Brousseau et al. 1982) and in the age-specific fecundity and survivorship rates of the soft-shell clam, *Mya arenaria*, using a modified Leslie matrix model and an extension of the sensitivity formulae derived by Caswell (1978). Predictions concerning the effect that changes in these life history parameters will have on λ and the implications of these results to the management of this species are discussed.

Results

Leslie Model

The population of females is divided into n age classes. The Leslie matrix, M, has the following form:

$$M = \begin{bmatrix} a_1 & a_2 & a_3 & \dots & a_{n-1} & a_n \\ r_s b_1 & 0 & 0 & \dots & 0 & 0 \\ 0 & b_2 & 0 & \dots & 0 & 0 \\ \vdots & \vdots & \vdots & & \vdots & \vdots \\ 0 & 0 & 0 & & b_{n-1} & 0 \end{bmatrix} \quad (1)$$

Here, a_i is the mean number of female eggs produced annually by a female in class i (age $i-1$ to i); assuming a one-to-one sex ratio, a_i is one-half the total egg production. The parameter b_i is the probability of a clam in class i surviving to class 2, 3, ..., $n-1$. The survivorship from age class 1 to age class 2 is divided into 2 factors, r_s and b_1. The factor r_s is the settlement rate or the probability that an egg will survive the planktonic larval stage and develop into a clam with a 2 mm shell length (0-2 mo of age); b_1 is the probability that a clam with a 2 mm shell length will survive the remainder of the year (about 10 mo). If x is a column vector with n components such that x_i is the number of females in age class i immediately following spawning, then Mx represents the population 1 yr from now.

For benthic marine invertebrates possessing planktotrophic larval stages, the events surrounding metamorphosis and settlement are extremely

important for the development and maintenance of species populations. Settlement rates are notoriously variable in nature, however, making it impossible to determine a fixed r_s and hence a fixed λ. For this reason, we have studied sensitivities over a range of λ's (0.25-3.0). Values of a_i and b_i used for *Mya arenaria* are empirically derived (Brousseau 1978a, b).

Sensitivity Formulae

The population growth rate, λ, is the eigenvalue of M with maximum modulus. In general, λ is unique and is a positive real number. This follows from the Perron-Frobenius Theorem, which may be referenced, for example, in Demetrius (1969). The sensitivity of λ to a life history parameter is defined to be the derivative of λ with respect to that parameter.

Following Caswell (1978), let u and v be column vectors satisfying

$$Mv = \lambda v \tag{2}$$

$$u'M = \lambda u' \tag{3}$$

$$(u, v) = 1 \tag{4}$$

where u' denotes the transpose of u, and $(\cdot,\cdot)$ denotes inner product. Statement (2) indicates that v is a right eigenvector while Statement (3) indicates that u is a left eigenvector, each associated with λ. Statement (4) is used as a normalization device. While Statements (2) through (4) do not define u and v uniquely, they are sufficient to make the sensitivity formulae below well defined. Explicit calculations for the components of vectors u and v start with

$$u_1 = 1$$

$$u_i = \sum_{j=1}^{n} a_j b_{j-1} \ldots b_i \lambda^{-(j-i+1)}, \; i > 1 \tag{5}$$

and

$$v_1 = 1$$

$$v_i = \lambda^{-i} b_{i-1} \ldots b_1 r_s, \; i > 1 \tag{6}$$

and then normalize using Statement (4) above.

With these definitions, Caswell (1978) shows

$$d\lambda/dm_{ij} = u_i v_j, \quad i,j = 1 \ldots n, \tag{7}$$

where m_{ij} is the parameter in the i,j position of the Leslie matrix M, u_i is the ith component of vector u_1, and v_j is the jth component of vector v. Of course, the components of M of interest to us are those in the first row (the fecundity parameters) and those in the main subdiagonal (the survivorship parameters). Further, since position m_{21} equals $r_s b_1$ in our notation, the sensitivity formulae become

$$d\lambda/da_i = u_1 v_i, \quad i = 1, 2, \ldots, n \tag{8}$$

$$d\lambda/db_i = u_{i+1} v_i, \quad i = 2, 3, \ldots, n-1 \tag{9}$$

$$d\lambda/db_1 = r_s d\lambda/dm_{21} = r_s u_2 v_1 \tag{10}$$

$$d\lambda/dr_s = b_1 d\lambda/dm_{21} = b_1 u_2 v_1. \tag{11}$$

In particular, notice that λ is not equally sensitive to r_s and b_1 unless the two values are equal.

For the present study, we hold a_i and b_i fixed and allow λ to vary. The settlement rate, r_s, then becomes a function of λ, specifically,

$$r_s = (\lambda - a_1)/(\lambda^{-1} a_2 b_1 + \lambda^{-2} a_3 b_2 b_1 + \ldots + \lambda^{-n+1} a_n b_{n-1} \ldots b_1), \tag{12}$$

and is used in the Leslie matrix, M. We then compute u and v satisfying Statements (2)-(4) for the given λ, and the sensitivity values Statements (8)-(11).

Relationships among the sensitivity formulae above have been derived by Demetrius (1969) and Caswell (1978). Of particular interest are

$$\begin{aligned} &d\lambda/da_i > d\lambda/da_j, \quad i < j, \lambda > 1 \\ &d\lambda/da_i < d\lambda/da_j, \quad i < j, \lambda < 1 \end{aligned} \tag{13}$$

$$b_i d\lambda/db_i > b_j d\lambda/db_j, \quad i < j \tag{14}$$

$$\frac{d\lambda/db_1}{d\lambda/da_1} = \frac{\lambda - a_1}{b_1}. \tag{15}$$

Statement (13) can actually be made stronger, as proven by Demetrius (1969, Statement (8)); Statement (14), in the case $i = 1$, and Statement (15) follow from Demetrius (1969, Statement (11)) and Caswell (1978, Statement (22)); and Statements (5), (10), and (12) above.

Calculation of Sensitivity Values

Settlement Rate.—Using the data in Table 1, the sensitivity of the population growth rate of

TABLE 1.—Life history statistics used in the derivation of the Leslie matrix for *Mya arenaria* (data from Brousseau 1978a, b).

Age (yr)	Age class	Shell length (mm)	Fecundity[1] (a_i)	Probability of survival (b_i)
0-1	1	2.0-29.9	0.0	0.177
1-2	2	30.0-44.9	3,744.0	0.912
2-3	3	45.0-59.9	17,170.0	0.904
3-4	4	60.0-64.9	31,159.0	0.952
4-5	5	65.0-69.9	39,957.0	0.949
5-6	6	70.0-74.9	50,341.0	0.969
6-7	7	75.0-79.9	62,450.0	0.984
7+	8+	80.0-84.9	76,465.0	0.911

[1]Fecundity = number of female eggs produced per individual assuming a 1:1 sex ratio.

Mya arenaria to changes in the settlement rate (r_s) can be calculated. Results are summarized in Table 2 for a range of values of λ. As expected, r_s increases as the population growth rate increases, while the sensitivity of λ to changes in r_s decreases as λ increases. The population growth rate, λ, is far more sensitive to changes in r_s than it is to changes in any other single life history parameter. A further discussion of this point is given below.

TABLE 2.—Sensitivity of various population growth rates (λ) to changes in the settlement rate (r_s). The intrinsic growth rate = $\log \lambda$.

Population growth rate (λ)	Intrinsic growth rate	Settlement rate (r_S)	Sensitivity of λ to r_S
0.25	−1.386	6.535×10^{-12}	3.291×10^{9}
0.5	−0.693	1.700×10^{-8}	2.697×10^{6}
0.75	−0.288	1.139×10^{-6}	6.822×10^{4}
1.0	0.0	[1]1.462×10^{-5}	8.562×10^{3}
1.25	0.223	7.320×10^{-5}	2.646×10^{3}
1.5	0.405	2.141×10^{-4}	1.307×10^{3}
1.75	0.560	4.618×10^{-4}	8.158×10^{2}
2.0	0.693	8.310×10^{-4}	5.765×10^{2}
3.0	1.099	3.702×10^{-3}	2.454×10^{2}

[1]r_S = Equilibrium settlement rate, $r_{S\,eq}$.

Fecundity and Other Survivorship Rates.—The sensitivity of λ to changes in fecundity are illustrated in Figure 1. Under equilibrium conditions ($\lambda = 1.0$), sensitivity to fecundity changes over the reproductive life span of the individual are slight. If the population is actually growing ($\lambda > 1.0$), the magnitude of the sensitivity to changes in the fecundity decreases with increasing age, while the reverse is true if the population is actually declining ($\lambda < 1.0$). This follows from Statement (13). For declining populations this is probably due to the combined effects of an increasing reproductive value with increasing age and a shift in the age structure to older individuals as the population declines.

The sensitivity of λ to changes in survivorship parameters other than r_s is illustrated in Figure 2, where it is evident that λ is more sensitive to changes in b_1, the survivorship of an individual from 2 mo to 1 yr of age, than to other values of b_i for $i > 1$. As above, these curves illustrate a general result. Since b_i is $> b_1$ for $i > 1$ in the *Mya arenaria* model, $d\lambda/db_1$ is $> d\lambda/db_i$ using Statement (14).

By comparing Figures 1 and 2, it seems evident that the population growth rate is more sensitive to changes in survivorship than to changes in fecundity. This result may be made precise if the population is actually growing ($\lambda > 1$), since using Statements (13) and (15) it follows that $d\lambda/db_1$ is $> d\lambda/da_i$ for all values of i. Finally, by examining Statements (10) and (11), it is clear that λ is more sensitive to r_s than to b_1 for the *Mya arenaria* model as long as r_s is $< b_1$. Hence, λ is more sensitive to r_s than to all other survivorship parameters, and, at least for growing populations, more sensitive to changes in r_s than to any other fecundity parameter as well.

Discussion

Fisher (1958) in his fundamental theorem of

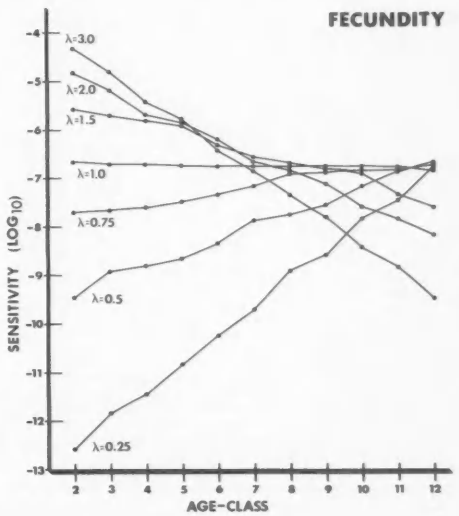

FIGURE 1.—Sensitivity of a range of λ's (0.25-3.0) to changes in the fecundity (a_i) of *Mya arenaria* in each age class. The first age class is not included since *Mya arenaria* are not mature until after the first year of age.

natural selection states that natural selection will favor genotypes which increase the population growth rate, λ. Since the λ for a population is based on the life history parameters of age-specific fecundity and survivorship, the greater the sensitivity of λ to changes in a particular life history value, the greater the potential for effecting evolutionary change through that parameter.

Existing evidence indicates that population growth rate is more sensitive to changes in survival rates than to changes in reproductive output. Cole (1954) reached this conclusion when he suggested that in species with repeated reproduction and relatively large litter size, there is little selection pressure favoring increased fecundity. Similarly, Caswell (1978) using Hartshorn's (1975) data for *Pentaclethra macroloba*, a tropical rain forest tree, illustrates by the use of models, that, for this species, population growth rate is more sensitive to changes in growth and survival than to changes in fecundity. The data reported here for *Mya arenaria* follow the same pattern; λ is relatively insensitive to changes in egg production. The most interesting results of the sensitivity analyses are produced by changes in the survivorship parameters.

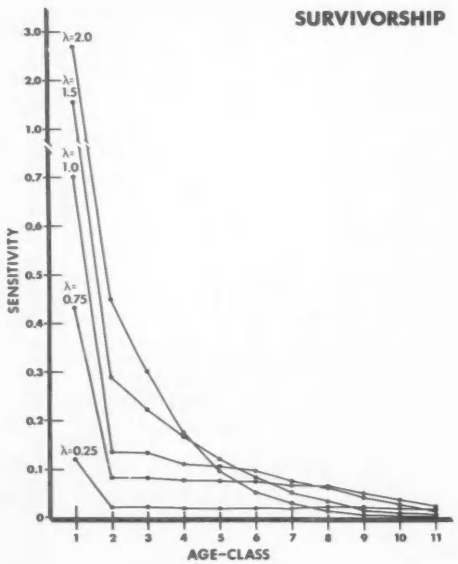

FIGURE 2.—Sensitivity of a range of λ's (0.25-2.0) to changes in the survivorship (b_i) of *Mya arenaria* in each age class.

Based on our analyses, two important generalizations can be made regarding the sensitivity of λ. First, whenever $r_s < b_1 < b_i$, the population growth rate will be more sensitive to changes in r_s than to changes in any of the other survivorship parameters. Second, in growing populations, i.e., where $\lambda > 1$, λ is always most sensitive to changes in the settlement rate. In terms of Deevey's (1947) categorization of generalized survivorship curves, the relationship $r_s < b_1 < b_i$ is probably operative in most Type III curves, which are characterized by extremely heavy mortality early in life. Consequently, these generalizations are of interest since the types of life history features exhibited by *Mya arenaria* are likely to be common to other species of marine organisms, many of which are also commercially important.

On a more practical level, the ability to identify those life history stages to which the population growth rate is most sensitive may serve as a useful tool in directing the efforts of those interested in shellfish management. For instance, the models described here indicate that larval settlement is the most critical stage in *Mya arenaria*'s life history. Developing a better understanding of the factors surrounding metamorphosis and settlement and implementing a method for inducing spatfall would probably be the single most effective way to increase clam yields.

Another area for consideration centers around the survivorship of the first year class. Since the population growth rate of *Mya arenaria* is also very sensitive to changes in the b_1 parameter, a second way to increase clam productivity is to improve the survivorship of clams 2 mo to 1 yr of age (ca. 2-25 mm shell length). This age class corresponds to that postlarval stage in *Mya arenaria* which is the most vulnerable to both biotic (predation) and abiotic (wash-out, temperature and salinity fluctuations) factors in the environment.

The practice of transplanting juvenile *Mya arenaria* from one flat to another has been used by managers since the turn of the century (Belding 1930) in efforts to 1) replenish depleted clam beds or 2) reduce densities in "overcrowded" beds. Currently, there is a renewed interest in this procedure[1] even though in the past, these efforts have met with varying degrees of success (Belding 1930; Turner 1951; Smith et al. 1955). The

[1]D. E. Wallace, Director, Department of Marine Resources, State of Maine, Boothbay Harbor, ME 04538, pers. commun. April 1983.

reasons may be related to the vulnerability of juveniles as discussed above.

To insure success with transplanting techniques, it is essential to reduce mortality among transplanted clams either by protecting them from significant sources of mortality in the field or by retaining them in protective "nurseries" until they pass this critical phase. Past attempts to protect juveniles in the field by building fences to exclude predators have proven costly, difficult to carry out, and unreliable (Smith et al. 1955). More promising are recent advances in aquaculture techniques for commercially important bivalves. By employing "nurseries" for the young and field "grow-out" procedures for adults, sources of juvenile mortality can be reduced while still utilizing natural sources of food during the greater part of the individual's growth period.

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THE OCCURRENCE OF PISCINE ERYTHROCYTIC NECROSIS (PEN) IN THE SEA LAMPREY, *PETROMYZON MARINUS*, FROM SEVERAL MAINE LOCALITIES

The sea lamprey, *Petromyzon marinus*, is an anadromous fish found in the North Atlantic Ocean from Iceland and northern Europe to northwestern Africa, and from the Grand Banks and the Gulf of St. Lawrence to Florida (Hubbs and Lagler 1949). The sea lamprey has adopted an entirely freshwater life cycle in the Great Lakes where it has seriously depleted fish populations (Everhart 1976).

The lamprey feeds on other fishes by hanging on with its sucking mouth. Once attached, it

rasps its victim with its tongue to obtain nourishment in the form of blood and other body fluids (Everhart 1976). Secretions from a pair of relatively large salivary glands below the tongue retard coagulation of host blood and also dissolve tissue (Lagler et al. 1977). Bigelow and Schroeder (1953) reported that in saltwater, lampreys have been found preying on mackerel, shad, cod, haddock, pollock, salmon, basking sharks, various anadromous herrings, swordfish, hake, sturgeons, and eels.

Piscine erythrocytic necrosis (PEN), a condition characterized by cytoplasmic inclusions and nuclear abnormalities in erythrocytes, has been shown to be of viral etiology in the Atlantic cod, *Gadus morhua*, and Atlantic herring, *Clupea harengus harengus*, from the Atlantic coast and the chum salmon, *Oncorhynchus keta*, pink salmon, *O. gorbuscha*, and Pacific herring, *Clupea harengus pallasi*, from the Pacific coast of North America (Walker 1971; Appy et al. 1976; Walker and Sherburne 1977; Philippon et al. 1977; Reno et al. 1978; Evelyn and Traxler 1978; MacMillan and Mulcahy 1979). In addition, PEN has been reported in 15 other marine teleost species from the Atlantic coast of North America, but confirmation as to viral etiology has not been made (Laird and Bullock 1969; Walker and Sherburne 1977; Sherburne 1977; Sherburne and Bean 1979). PEN has also been evident in the Atlantic mackerel, *Scomber scombrus*, (Sherburne, unpubl. data).

This report documents the first finding of PEN in a host from the most primitive group of fishes, the Agnatha.

Materials and Methods

A total of 142 lampreys, *Petromyzon marinus*, was obtained for blood analysis from 5 Maine localities (Table 1). Live lampreys were measured for total length and sexed. Slides were prepared by severing the caudal peduncle and taking the blood into a heparinized capillary tube, from which a small drop of blood was placed on a microscope slide and the smear made. Air-dried smears were Giemsa-stained and thoroughly examined for PEN using light microscopy at 1000× magnification.

Results

Of the total lampreys sampled in this study, 50.7% (72/142) had red cell lesions characteristic of PEN (Table 1). By light microscopy, PEN lesions of lamprey red cells often showed the nuclear chromatin condensed into round blebs, and there was evidence of nuclear vacuolization (Fig. 1). Red acidophilic cytoplasmic inclusions were occasionally seen in an infected cell (Fig. 2).

Individual infections were light, with only one or two infected cells evident in most smears. Among the 72 infected lampreys, the severest infection involved 2% of the red cells and it occurred in a 69 cm male from the Coopers Mills Fishway on 26 May 1980.

From a total of 139 lampreys sexed, 47.9% of the males and 53.0% of the females had PEN. The smallest infected lamprey was 62.4 cm (24.6 in) long; the largest was 81.5 cm (32.1 in).

TABLE 1.—The occurrence of piscine erythrocytic necrosis (PEN) in the sea lamprey, *Petromyzon marinus*, from several Maine localities.

Sample source	Location	Date	PEN		Mean length, SD, and range (cm) of sample
			Incidence in sample	Percent incidence	
Nequasset Lake Fishway	Woolwich	16 June 1977	0/2	0.0	67.0 ± 1.4 (66.0 – 68.0)
Kennebunk River	Kennebunk	11 May 1978	1/1	100	63.1 (63.1)
Sheepscot Pond Fishway	Palermo	9 June 1978	1/3	33.3	65.4 ± 2.7 (62.5 – 67.8)
Sheepscot Pond Fishway	Palermo	15 June 1978	0/1	0.0	65 (65)
Sheepscot River Coopers Mills Fishway	Coopers Mills	30 May 1979	5/28	17.8	72.4 ± 4.1 (62.4 – 82)
Sheepscot River Coopers Mills Fishway	Coopers Mills	26 May 1980	34/46	73.9	72.4 ± 4.6 (66 – 88.5)
Sheepscot River Head Tide	Alna	6 June 1983	7/18	38.8	71.4 ± 4.3 (64.8 – 78.8)
Sheepscot River Coopers Mills Fishway	Coopers Mills	13 June 1983	1/4	25.0	73.5 ± 2.3 (70.0 – 75.0)
Sheepscot River Head Tide	Alna	14 June 1983	5/8	62.5	70.6 ± 3.4 (66.7 – 76.0)
Sheepscot River Head Tide	Alna	15 June 1983	18/31	58.1	70.5 ± 4.0 (63.5 – 78.0)

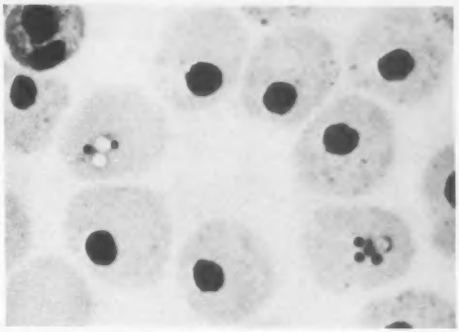

FIGURE 1.—Sea lamprey erythrocytes with PEN lesions. Infected cells show characteristic chromatin condensation with evidence of nuclear vacuolization. From a female lamprey 80 cm in total length from the Coopers Mills Fishway, Coopers Mills, Me., on 26 May 1980. Sea lamprey erythrocytes are rounded in shape in contrast to most other fish species which have elliptical shaped red cells.

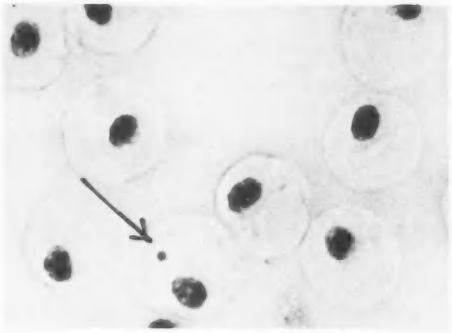

FIGURE 2.—Red acidophilic inclusions are occasionally seen in PEN infected sea lamprey erythrocytes. From a female lamprey 67.8 cm in total length from the Sheepscot Pond Fishway, Palermo, Me., on 9 June 1978.

Discussion

I prefer to use the term PEN in species where the cellular pathology has not yet been confirmed as associated with a virus, and viral erythrocytic necrosis (VEN) after confirmation. By light microscopy, PEN lesions of lamprey red cells resemble those of VEN-infected Atlantic cod. As with alewives, *Alosa pseudoharengus*, (Sherburne 1977) and smelt, *Osmerus mordax*, (Sherburne and Bean 1979), lampreys have a relatively high percentage of individuals affected with PEN, but individual infections are very light.

The blood of the sea lamprey must be examined by electron microscopy to determine if the PEN seen is an ICDV infection. Unfortunately, the individual infections observed in this study were so light as to preclude their detection by electron microscopy. Consequently, viral etiology of the condition still remains to be confirmed.

Fish obtained from lakes where alewives spawn have shown typical PEN lesions (Sherburne, unpubl. data), but whether alewives contribute to this is unknown. MacMillan and Mulcahy (1979) reported transferring VEN to chum salmon, *Oncorhynchus keta*, and brook trout, *Salvelinus fontinalis*, by waterborne virus. Perhaps infected anadromous species can transmit PEN to freshwater species via body fluids such as urine and reproductive products as well as by direct contact.

Lampreys could conceivably transmit PEN to a variety of marine and freshwater species because of their feeding habits, their diversity of prey, and their ability to become adapted to an entirely freshwater environment. The high prevalence of infection and the low intensity of infection suggest that lampreys might readily spread the infection without suffering a high mortality rate from PEN.

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ERRATA

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Livingston, P. A., "Food habits of Pacific whiting, *Merluccius productus*, off the west coast of North America, 1967 and 1980," p. 629-636.

Page 635, Equation (2) should read: $R = 0.0416e^{0.105T}$.

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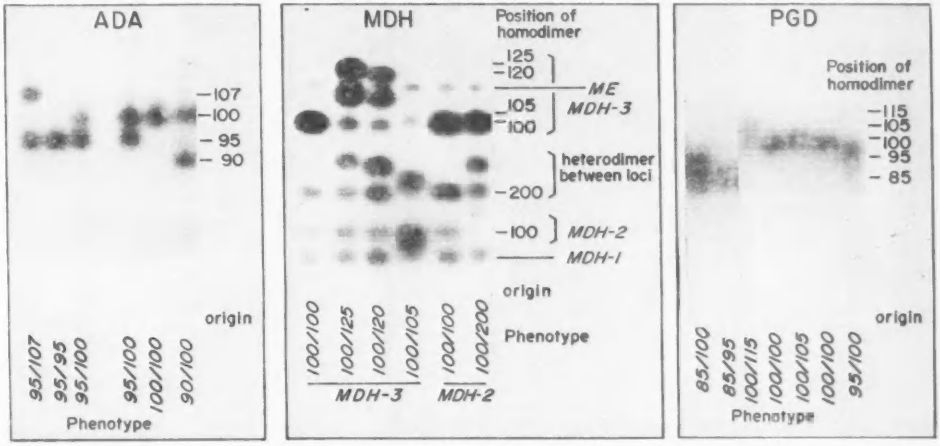
Grant, W. S., R. Bakkala, F. M. Utter, D. J. Teel, and T. Kobayashi, "Biochemical genetic population structure of yellowfin sole, *Limanda aspera*, of the North Pacific Ocean and Bering Sea," p. 667-677.

Page 672, Figure 2, the top portion should read:



Sherman, K., J. R. Green, J. R. Goulet, and L. Ejsymont, "Coherence in zooplankton of a large northwest Alantic ecosystem," p. 855-862.

Pages 858 and 889 should read:

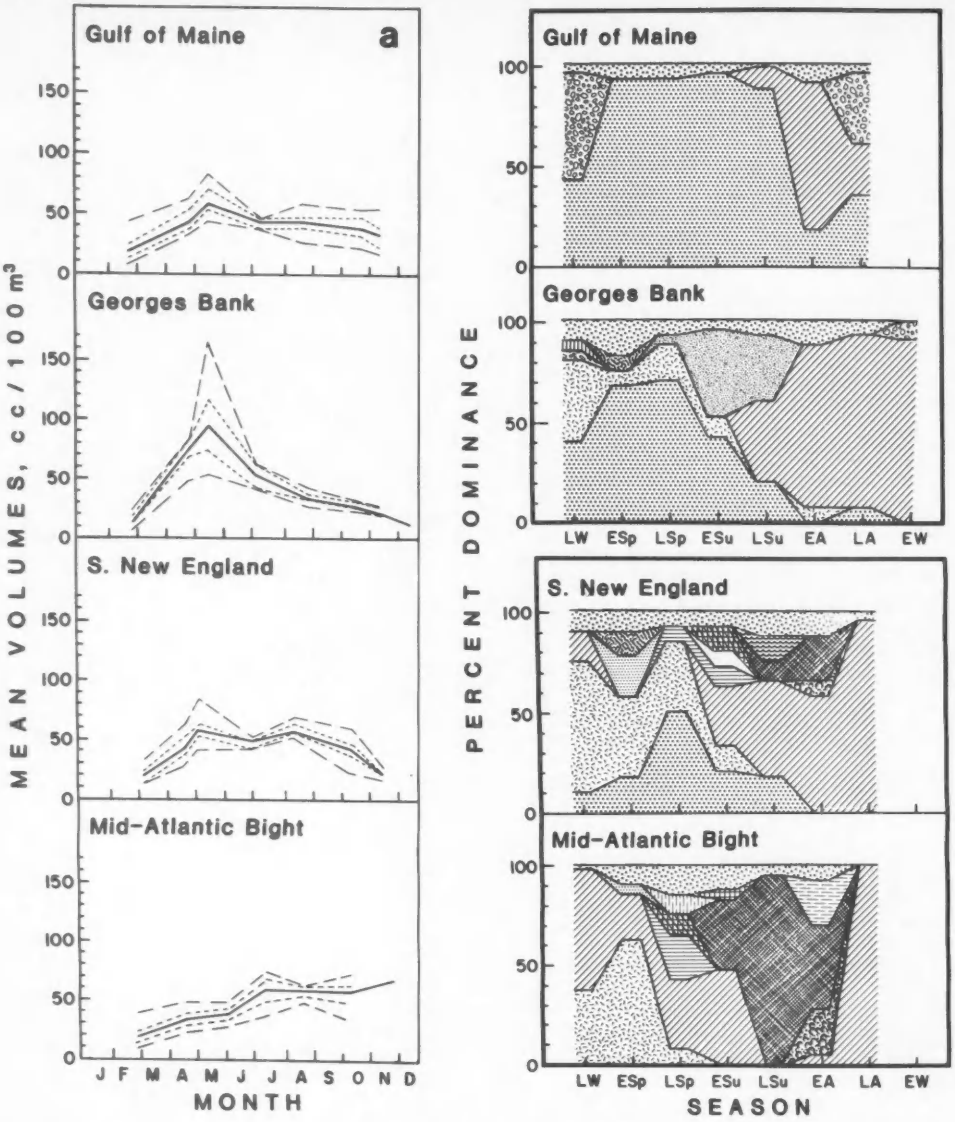


FIGURE 2.—Patterns of zooplankton in four northeastern U.S. continental shelf subareas—Gulf of Maine, Georges Bank, Southern New England, and the Mid-Atlantic Bight. (a) Seasonal patterns in mean zooplankton standing stock (cc/100 m^3) for the 5-yr MARMAP time series. Solid line represents the mean, short dashed line is one standard duration, and long dashed line is the range.

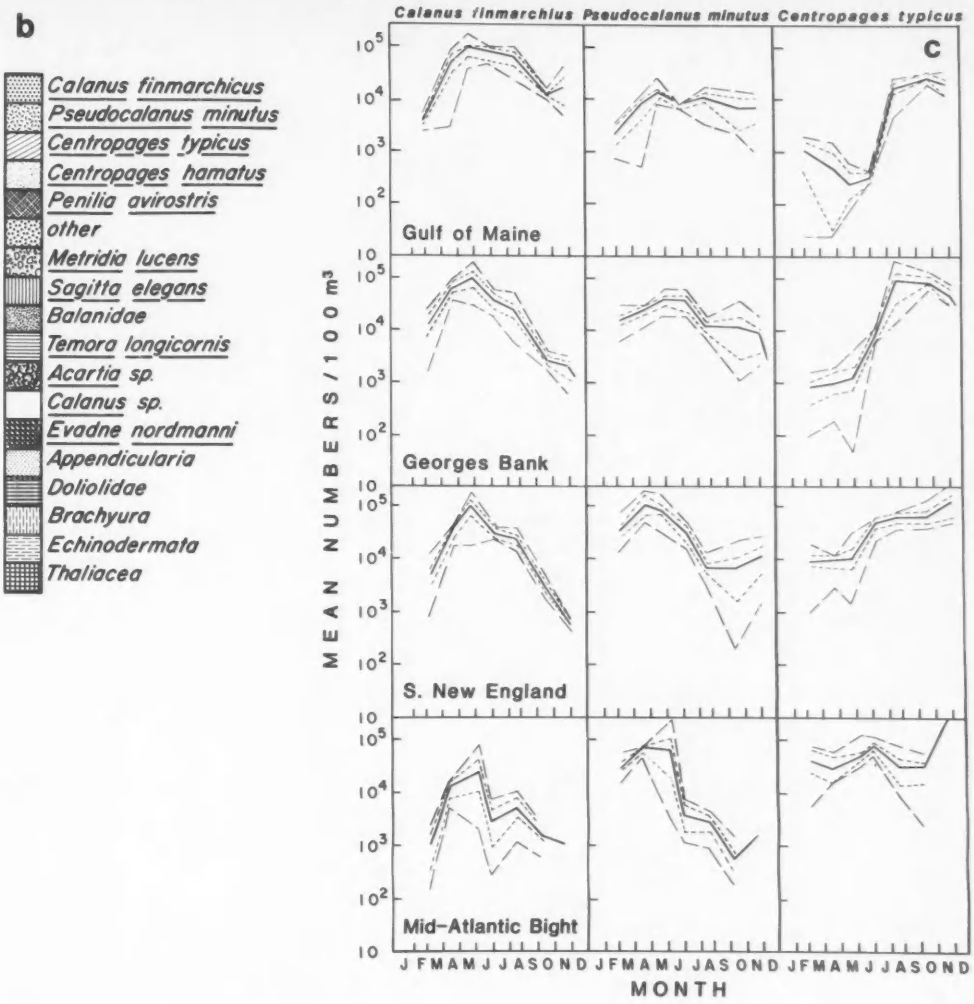


FIGURE 2.—*Continued*—(b) Seasonal patterns of dominance of zooplankters by subarea shown as a percentage of the samples with a dominant taxon in the 5-yr MARMAP time series. LW = late winter, ESp = early spring, ESu = early summer, EA = early autumn, LA = late autumn, and EW = early winter. (c) Seasonal pulses in abundance of the three dominant copepod species *Calanus finmarchicus*, *Pseudocalanus minutus*, and *Centropages typicus* (No./100 m³) in each of the subareas for the 5-yr time series. Solid line represents the mean, short dashed line is one standard duration, and long dashed line is the range.

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